ECOLOGICAL EFFECTS OF INVASIVE EUROPEAN BIRD CHERRY (*PRUNUS PADUS*) ON SALMONID FOOD WEBS IN ANCHORAGE, ALASKA STREAMS

By

David A. Roon

RECOMMENDED:

Anupma Prakash, Ph.D.

Tricia Wurtz, Ph.D.

Mark Wipfli, Ph.D.
Advisory Committee Chair

Christa Mulder, Ph.D.
Chair, Department of Biology and Wildlife

APPROVED:

Paul Layer, Ph.D.
Dean, College of Natural Science and Mathematics

Lawrence Duffy, Ph.D.
Dean of the Graduate School

Date

ECOLOGICAL EFFECTS OF INVASIVE EUROPEAN BIRD CHERRY (*PRUNUS PADUS*) ON SALMONID FOOD WEBS IN ANCHORAGE, ALASKA STREAMS

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By

David A. Roon, B.A.

Fairbanks, Alaska

August 2011

Abstract

Invasive species are a concern worldwide as they can displace native species, reduce biodiversity, and disrupt ecological processes. European bird cherry (*Prunus padus*) (EBC) is an invasive ornamental tree that is rapidly spreading and possibly displacing native trees along streams in parts of urban Alaska. The objectives of this study were to: 1) map the current distribution of EBC along two Anchorage streams, Campbell and Chester creeks, and 2) determine the effects of EBC on selected ecological processes linked to stream salmonid food webs. Data from the 2009 and 2010 field seasons showed: EBC was widely distributed along Campbell and Chester creeks; EBC leaf litter in streams broke down rapidly and supported similar shredder communities to native tree species; and EBC foliage supported significantly less terrestrial invertebrate biomass relative to native deciduous tree species, and contributed significantly less terrestrial invertebrate biomass to streams compared to mixed native vegetation, but riparian EBC did not appear to affect the amount of terrestrial invertebrate prey ingested by juvenile coho salmon (*Oncorhynchus kisutch*). Although ecological processes did not seem to be dramatically affected by EBC presence, lowered prey abundance as measured in this study may have long-term consequences for stream-rearing fishes as EBC continues to spread over time.

Table of Contents

Page
Signature Page ... i
Title Page ... ii
Abstract ... iii
Table of Contents ... iv
List of Figures ... vii
List of Tables ... viii
Acknowledgements ... ix
Introduction ... 1
    Influence of riparian vegetation on stream salmonid food webs ... 1
    Riparian vegetation type can affect invertebrate prey for stream salmonids ... 3
    Effects of invasive riparian plants on stream food webs ... 5
    Potential effects of European bird cherry on salmonid food webs ... 8
    References ... 9
Chapter 1: The abundance and distribution of invasive *Prunus* spp. in riparian forests along streams in Anchorage, Alaska ... 16
    Abstract ... 16
    Introduction ... 17
    Study Site ... 18
    Methods ... 18
    Results ... 20
    Discussion ... 21
    Acknowledgements ... 24
    References ... 24
Chapter 2: Leaf litter processing is similar between native plants and invasive European bird cherry in urban Alaskan streams ... 32
    Summary ... 32

Introduction 33
Methods 35
  Study area 35
  Study site characteristics 36
  Leaf pack experiments 36
  Laboratory procedures 37
  Statistical analysis 38
Results 39
  Study site characteristics 39
  Leaf litter breakdown 39
  Aquatic invertebrate shredders 40
Discussion 42
Acknowledgements 46
References 47
Chapter 3: Invasive European bird cherry disrupts stream-riparian linkages: influence on terrestrial invertebrate prey subsidies for juvenile coho salmon 62
Abstract 62
Introduction 63
Methods 66
  Study sites 66
  Site characterization 66
  Terrestrial invertebrates associated with riparian trees 67
  Stream inputs of terrestrial invertebrates 67
  Juvenile coho salmon ingestion of terrestrial invertebrates 68
  Statistical analysis 69
Results 70
  Site characteristics 70
  Terrestrial invertebrates associated with riparian trees 70
  Stream inputs of terrestrial invertebrates 71

Juvenile coho salmon ingestion of terrestrial invertebrates 72
Community structure and overlap between prey availability and coho diet 73
Discussion 74
Acknowledgements 80
References 80
Conclusion 97
References 100

List of Figures

Page

Figure 1.1. Distribution of *Prunus padus* along Chester and Campbell creeks............... 30

Figure 1.2. Distribution of *Prunus virginiana* along Chester and Campbell creeks........ 31

Figure 2.1. Map of leaf pack study sites in Campbell and Chester creeks 56

Figure 2.2. Breakdown of EBC and native leaf litter in Chester Creek in 2009 57

Figure 2.3. Breakdown of EBC and alder leaf litter in Campbell and Chester creeks in 2010.. 58

Figure 2.4. Abundance and biomass of aquatic invertebrate shredders in 2009.............. 59

Figure 2.5. Abundance and biomass of aquatic invertebrate shredders in 2010.............. 60

Figure 2.6. Community structure of aquatic invertebrate shredders................................ 61

Figure 3.1. Map of EBC and native vegetation study sites in Campbell and Chester creeks 90

Figure 3.2. Terrestrial invertebrate biomass associated with foliage of riparian tree branches 91

Figure 3.3. Stream inputs of terrestrial invertebrate biomass 92

Figure 3.4. Proportion of coho diet composed by terrestrial invertebrates...................... 93

Figure 3.5. Terrestrial invertebrate biomass ingested by juvenile coho salmon............... 94

Figure 3.6. Community structure of terrestrial invertebrates in 2009.............................. 95

Figure 3.7. Community structure of terrestrial invertebrates in 2010.............................. 96

List of Tables

Page

Table 1.1. Vegetation data from Chester Creek plots 27

Table 1.2. Vegetation data from Campbell Creek plots.. 28

Table 1.3. *Prunus* succession levels along Chester and Campbell creeks 29

Table 2.1. Study site characteristics of leaf pack experiments in Campbell and Chester creeks 52

Table 2.2. Breakdown rates (*k*) of EBC and native leaf litter 53

Table 2.3. Shredder composition associated with EBC and native leaf litter.................. 54

Table 2.4. Shredder growth associated with EBC and native leaf litter 55

Table 3.1. Characteristics of EBC and native vegetation study sites in Campbell and Chester creeks 86

Table 3.2. Terrestrial invertebrate community composition in 2009............................... 87

Table 3.3. Terrestrial invertebrate community composition in 2010............................... 88

Table 3.4. Overlap of terrestrial invertebrate communities 89

Acknowledgements

There are a lot of people who helped me through the course of this project. First, I’d like to credit my advisor, Mark Wipfli, and committee members, Tricia Wurtz and Anupma Prakash, for their guidance, encouragement and support throughout this process.

I am very grateful to all the people who helped me collect data in the field and process invertebrate samples in the lab. Assisting me in the urban wilderness of Anchorage were Dustin Merrigan, John Hill, Steve Ewest, Rebecca Mierzejewski, Michael Rasy and Ashley Grant. Back in Fairbanks, Uinniq Ahgeak and Thomas Robertson joined for long hours at the microscope processing fish puke samples.

At University of Alaska Fairbanks, the members of the Wipfli aquatics lab were close friends and invaluable resources. Thanks to Bessie Green, Laura Gutierrez, Megan Perry, Emily Benson, Jason Neuswanger, Stephanie Fisher and Jason McFarland. Arny Blanchard contributed many hours in and outside of class helping with the statistics for this project. Derek Sikes’ superior insect knowledge helped me identify unknown specimens.

Thanks to the many project collaborators who helped get the project off the ground while in Anchorage. Dan Rinella and Dan Bogan at Environment and Natural Resources Institute provided summer lab space and shared their in depth knowledge of stream invertebrates. Matt Carlson, Helen Cortés-Burns and Lindsey Flagstad at the Alaska Natural Heritage Program helped design the bird cherry survey protocol. Michael Rasy at the UAF Cooperative Extension Service helped with the initial reconnaissance of the study streams and acted as a resource for all things insect and invasive species related.

Finally, thanks to all my funding sources, including Jeff Heys and David Wigglesworth at US Fish and Wildlife Service, USDA Forest Service, Alaska EPSCoR, Institute of Arctic Biology, and the Department of Biology and Wildlife at UAF.

All chapters have been prepared as manuscripts for publication. Chapter 1 will be submitted to Biological Invasions and co-authors include David Roon, Mark Wipfli (UAF), Tricia Wurtz (USFS), and Anupma Prakash (UAF). Chapter 2 will be submitted

to Freshwater Biology and co-authors include David Roon, Mark Wipfli (UAF), and Tricia Wurtz (USFS). Chapter 3 will be submitted to Canadian Journal of Fisheries and Aquatic Sciences and co-authors include David Roon, Mark Wipfli (UAF), Tricia Wurtz (USFS), and Arny Blanchard (UAF). David Roon designed the study, collected and analyzed the data and wrote the manuscripts for all three chapters. Mark Wipfli developed the initial questions addressed in this study, offered input during the planning stages, reviewed the manuscripts and supervised the entire process for all chapters. Tricia Wurtz developed the initial questions, offered input during the entire process and reviewed the manuscripts. Anupma Prakash assisted with the mapping analysis in chapter 1, offered input during the process and reviewed the manuscripts. Arny Blanchard assisted with statistical analyses and reviewed chapter 3.

Introduction

Influence of riparian vegetation on stream salmonid food webs

Although accounting for only a small portion of overall landcover, riparian zones are important ecologically, acting as dynamic interfaces that link terrestrial and aquatic ecosystems (Gregory et al. 1991). Much research has focused on the influence of riparian forests in regulating the physical habitats of their associated stream and river systems for stream fishes (Wipfli and Baxter 2010). For example, shade from the riparian canopy controls the light reaching the stream channel, affecting stream temperature (Gregory et al. 1991). Roots of riparian trees stabilize streambanks, regulating terrestrial sediment inputs important for spawning and rearing habitats (Bilby and Ward 1991). Fallen trees supply woody debris to streams and rivers, which mixes instream flow creating pool habitats that act as refugia for rearing juveniles (Bilby and Ward 1991, Tabacchi et al. 1998). Finally, research has also detailed the importance of riparian vegetation as a source of energy for stream organisms supporting salmonid food webs (Gregory et al. 1991, Wallace et al. 1997, Nakano and Murakami 2001, Baxter et al. 2005).

Small or low-order stream ecosystems are often considered to be energy-limited and depend on external or *allochthonous* inputs of organic matter (e.g. detritus and insects) from the adjacent terrestrial ecosystem as primary sources of energy supporting salmonid food webs (Vannote et al. 1980, Wallace et al. 1997). Two pathways link riparian vegetation to stream salmonids: 1) senesced leaf litter inputs from riparian vegetation are processed by aquatic invertebrate detritivores (termed “shredders”), supporting entire aquatic invertebrate communities; and 2) terrestrial invertebrates from the adjacent riparian vegetation fall directly into the stream. The combination of these invertebrate communities compose the primary prey resources for salmonids and other stream fishes (Wipfli 1997, Nakano and Murakami 2001, Baxter et al. 2005).

In the first pathway, senesced leaf litter from the riparian vegetation enters the stream channel where aquatic bacteria and fungi colonize the leaf surfaces conditioning the leaf litter (Vannote et al. 1980, Cummins et al. 1989). Functional feeding groups of aquatic invertebrates adapted to feed on detritus, collectively called *shredders*, then feed on the vascular tissue of the conditioned leaf litter (Vannote et al. 1980, Cummins et al. 1989, Wallace et al. 1997). Vannote et al.'s (1980) *river continuum concept* hypothesized that low-order streams support high densities of shredders due to large volumes of leaf litter inputs from overhanging riparian canopies of deciduous trees (Peterson and Cummins 1974, Webster and Benfield 1986). Leaf litter processing by shredders breaks down leaf litter inputs into coarse and fine particles of organic matter for other functional feeding groups of aquatic invertebrates (Peterson and Cummins 1974, Cummins et al. 1989, Wallace et al. 1997). As a result, shredders play an important functional role in streams, supporting diverse aquatic invertebrate communities which collectively act as prey for many upper trophic level consumers including stream fishes (Wallace et al. 1997, Gessner and Chauvet 2002, Baxter et al. 2005).

In the second pathway, terrestrial invertebrate communities associated with the foliage of the adjacent riparian vegetation fall directly into the stream channel (Wipfli 1997, Nakano and Murakami 2001, Kawaguchi et al. 2003). These invertebrates fall into the stream when searching for food and water or by accidentally dropping in from overhanging branches. Low-order streams with dense riparian canopies contribute high levels of terrestrial invertebrate biomass to streams (Wipfli 1997, Kawaguchi and Nakano 2001, Nakano and Murakami 2001, Baxter et al. 2005). Studies have also linked riparian canopy cover with stream inputs of terrestrial invertebrates and density in the drift (Meehan 1996, Allan et al. 2003, Romero et al. 2005). Terrestrial invertebrate abundance peaks in the warmest part of the year with the highest densities occurring spring through fall (Nakano and Murakami 2001, Baxter et al. 2005).

While it has been long established that salmonids drift feed on aquatic invertebrates (Allan 1978, Johnson and Ringler 1980), *Allen's paradox* pointed out that aquatic invertebrate production alone was insufficient to support fish in New Zealand streams (Allen 1951). More recent research has highlighted the importance of terrestrial invertebrates as a seasonal prey source that might help explain *Allen's paradox* (Johnson and Ringler 1980, Edwards and Huryn 1995, Wipfli 1997, Nakano and Murakami 2001, Kawaguchi and Nakano 2001, Allan et al. 2003, Kawaguchi et al. 2003). While aquatic invertebrates are important prey resources year round, salmonid predation on terrestrial invertebrates often peaks in the summer and fall (Nakano and Murakami 2001, Baxter et al. 2005). Wipfli (1997) reported terrestrial invertebrates composed up to 50% of the biomass in the diet for several species of stream salmonids in southeast Alaska. Kawaguchi and Nakano (2001) found terrestrial invertebrates composed 53% of prey ingested by salmonids in Japan. Some evidence suggests that salmonids may even prey selectively on terrestrial invertebrates (Nakano et al. 1999b).

Riparian vegetation type can affect invertebrate prey for stream salmonids

Vegetation type can affect both aquatic and terrestrial invertebrate communities. The *resource quality hypothesis* predicts that invertebrates will feed preferentially on plants that are higher-quality resources (Schowalter et al. 1986, Ober and Hayes 2008). Resource quality can be a combination of the chemical and physical characteristics of a plant species (Ober and Hayes 2008). Leaf chemistry can affect invertebrate herbivory through nutrient content and presence of secondary compounds (Cummins et al. 1989, Graça 2001). Physical characteristics like presence of structural compounds (e.g. lignin), leaf thickness and its ability to break down quickly can also affect herbivory by invertebrates. Aquatic invertebrate shredders can be influenced by leaf litter quality, selectively feeding on higher-quality leaf litter inputs (Graça 2001). Leaf litter that breaks down quickly in streams provides a readily available food source for shredders and is often correlated with high-quality leaf species (Irons et al. 1988, Cummins et al. 1989, Motomori et al. 2001). Feeding experiments have documented that nitrogen-rich species like alder support higher shredder abundances than other lower-quality species (Irons et al. 1988, Motomori et al. 2001).

Terrestrial invertebrate communities in riparian forests can also vary between vegetation types, affecting their abundance (Mason and MacDonald 1982, Ober and Hayes 2008). Studies in southeast Alaska and in Oregon documented an increased abundance of terrestrial invertebrates associated with nitrogen-rich deciduous trees (e.g.

alder) relative to coniferous trees (Meehan 1996, Wipfli 1997, Allan et al. 2003, Romero et al. 2005, Ober and Hayes 2008). This increased abundance of terrestrial invertebrates can lead to increased inputs of invertebrates to streams and their density in the drift in reaches of higher quality riparian vegetation (Wipfli 1997, Kawaguchi and Nakano 2001, Piccolo and Wipfli 2002, Allan et al. 2003, Romero et al. 2005).

As a result, riparian vegetation type can influence the availability of aquatic and terrestrial invertebrate prey resources for stream salmonids (Mason and MacDonald 1982, Wipfli 1997, Allan et al. 2003, Romero et al. 2005). For example, Kawaguchi and Nakano (2001) who observed increased trout biomass in forested streams compared to grassland streams in Japan. However, few other studies have actually documented an effect of vegetation type on the amount of prey ingested by stream fishes (Meehan 1996, Wipfli 1997, Kawaguchi and Nakano 2001, Allan et al. 2003, Romero et al. 2005). This indicates that an increase in prey resources does not necessarily result in a response by fish, suggesting fish may not be tracking resources or might not be food limited (Giannico and Healey 1999).

Experimentally altering terrestrial invertebrate resources has illustrated the ecological consequences for both terrestrial and aquatic organisms linked through stream-riparian food webs. A study by Kawaguchi et al. (2003) indicated that experimentally reducing terrestrial inputs to streams decreased the abundance and shifted the distribution of rainbow trout. Nakano et al. (1999a) found that reducing stream inputs of terrestrial invertebrates increased salmonid predation on aquatic invertebrate herbivores, which led to an increase in growth of benthic algae. A related study observed the invasion of non-native rainbow trout (*Oncorhynchus mykiss*) in Japanese streams competed with Dolly Varden charr (*Salvelinus malma*) for terrestrial invertebrates, forcing Dolly Varden to feed more heavily on aquatic invertebrates, decreasing the emergence of adult life stages of aquatic invertebrates (Baxter et al. 2004). This decrease in aquatic invertebrate emergence impacted riparian predators including spiders and birds (Baxter et al. 2004; Nakano and Murakami 2001). These results clearly show that changes in vegetation can affect invertebrate prey abundance for salmonids and that reducing the availability of invertebrate prey can negatively affect salmonids and other aquatic and terrestrial organisms linked through stream-riparian food webs.

Effects of invasive riparian plants on stream food webs

Riparian zones are highly susceptible to the spread of invasive plants (Gregory et al. 1991, Hood and Naiman 2000). The combination of flood events that disturb riparian soils and extensive habitat connectivity along riparian corridors creates ideal conditions for invasive plants to spread (Hood Naiman 2000). As a result, riparian forests often contain a higher number of invasive plants than upland habitats (Planty-Tabacchi et al. 1996, Hood and Naiman 2000). Invasive plants are a concern worldwide because they can displace native species, reduce biodiversity and disrupt ecological processes (Wilcove et al. 1998, Dukes and Mooney 1999). Invasive plants can grow in dense patches, outcompeting nearby native species for resources (e.g. light, water and nutrients) (Dangles et al. 2003, Friedman et al. 2005, Lecerf et al. 2007). They can also exhibit allelopathic properties, negatively affecting germination and growth of native species (Hierro and Callaway 2003). Because riparian zones link terrestrial and aquatic ecosystems, the spread of invasive plants in riparian forests can negatively affect stream organisms and food webs (Hood and Naiman 2000, Baxter et al. 2005).

One way the spread of invasive plants in riparian forests could affect stream food webs is by changing the composition of leaf litter inputs. By displacing native species invasive plants can reduce the species richness and overall quality of these leaf litter inputs (Hood and Naiman 2000, Dangles et al. 2003, Kennedy and Hobbie 2004, Lecerf et al. 2005 and Lecerf et al. 2007, Braatne et al. 2007). As invasive plants spread along the streambanks they compete with the native vegetation, often displacing native species. This changes the composition of leaf litter entering the stream channel, frequently reducing the richness of these allochthonous inputs (Dangles et al. 2003, Lecerf et al. 2007). Peterson and Cummins (1974) described the importance of having a processing continuum of resources available for stream consumers. Naeem et al. (1994) describes high species richness as essential to the health and function of an ecosystem. Declines in the species richness of riparian vegetation can affect the diversity of leaf litter available for stream consumers (Dangles et al. 2003, Lecerf et al. 2007).

If an invasive plant differs from native vegetation in leaf litter chemistry, it can affect leaf litter processing by aquatic invertebrate shredders (Graça 2001). Aquatic microorganisms responsible for conditioning leaf litter often are more likely to colonize higher-quality species (Irons et al. 1988, Cummins et al. 1989, Lecerf et al. 2007). Shredders in turn are more likely to feed on properly conditioned leaf litter (Cummins et al. 1989). Three invasive plants, eucalyptus (*Eucalyptus* spp.), Japanese knotweed (*Fallopia japonica*) and tamarisk (*Tamarix* spp.), have all been documented to break down more slowly than the leaf litter of native riparian plant species, suggesting that they are lower-quality food sources for stream consumers (Canhoto and Graça 1995, Abelho and Graça 1996, Bailey et al. 2001, Kennedy and Hobbie 2004, Braatne et al. 2007, Lecerf et al. 2007).

However, studies examining the effects of invasive plants on shredder feeding activity have documented variable, even conflicting results, sometimes with the same species (Canhoto and Graça 1995, Abelho and Graça 1996, Lacan et al. 2010). Some studies have documented declines in shredder abundance, diversity and growth associated with invasive plants like Japanese knotweed, eucalyptus, and tamarisk (Canhoto and Graça 1995, Abelho and Graça 1996, Read and Barmuta 1999, Bailey et al. 2001, Dangles et al. 2003, Lecerf et al. 2005, Lecerf et al. 2007). In contrast, other studies found no significant effect of invasive leaf litter on shredders (Sampaio et al. 2001, Braatne et al. 2007, Going and Dudley 2008, Moline and Poff 2008, Swan et al. 2008, Lacan et al. 2010). One can conclude from the variable results that while in some cases leaf litter quality can negatively affect shredder communities, invasive plants can sometimes act as a suitable or even superior resource for shredders. Graça (2001) determined that shredders fed on less-preferred plant species when no other choice is available and Cummins et al. (1989) concluded that the condition of leaf litter could be more important than the particular species composition.

The spread of invasive plants may also affect terrestrial invertebrates (Mason and MacDonald 1982, Ober and Hays 2008). Observational field studies have documented declines in terrestrial invertebrate abundance and species richness relative to native vegetation with invasive giant reed (*Arundo donax*) in California (Herrera and Dudley 2003), Japanese knotweed in Europe (Gerber et al. 2008) and tamarisk in the American southwest (Wiesenborn 2005). In addition to documenting declines of terrestrial invertebrate abundance, Greenwood et al. (2004) also found that relative to native vegetation invasive willow (*Salix rubens*) reduced stream inputs of terrestrial invertebrates to Australian streams.

Few studies have attempted to relate the effects of invasive riparian plants on invertebrate communities to stream food webs or to upper trophic level consumers like stream fishes. If an invasive plant in riparian forests reduces invertebrate prey abundance, then it could negatively affect invertebrate prey resources for stream salmonids, potentially affecting salmonid production in streams (Wipfli and Gregovich 2002). A study by Glova and Sagar (1994) in New Zealand found streams lined with invasive willow supported a higher abundance of invertebrate prey for brown trout than streams lined by native vegetation. In contrast, Kennedy et al. (2005) found that the eradication of invasive tamarisk increased fish densities in Colorado streams. Considering the conflicting results from these two studies, this topic warrants further investigation.

As invasive species continue to spread across landscapes, we need to understand their ecological effects. It is difficult to predict which invasive species will be problematic, as previous studies have found varying and even conflicting results sometimes within the same species (Abelho and Graça 1996, Lacan et al. 2010). This is especially true in Alaska, where until recently it was assumed invasive plants had little impact due to its geographic isolation (Carlson and Shephard 2007). Instead, a recent review found that invasive plants are becoming increasingly common around urban centers and are spreading into adjacent natural habitats (Carlson and Shephard 2007). In spite of this observation, research concerning the ecological effects of invasive species in Alaska remains lacking. This is especially true in riparian forests where the spread of invasive plants has the potential to affect both terrestrial and aquatic organisms and the exchange of resources between the two (Baxter et al. 2005).

In Alaska and around the Pacific Ocean, Pacific salmon (*Oncorhynchus* spp.) are important cultural, economic and ecological resources. Many Pacific salmon populations are currently experiencing significant declines and concern has been raised that invasive species could be a contributing factor (Baxter et al. 2005, Sanderson et al. 2009). Observational and experimental studies are needed to evaluate the ecological effects of invasive riparian plants on stream salmonids.

Potential effects of European bird cherry on salmonid food webs

European bird cherry (*Prunus padus*) (EBC) is an introduced deciduous tree frequently planted in Alaska for its showy floral display (Alaska Natural Heritage Program 2006). Birds feed on the cherries and transport the seeds from source trees to adjacent natural areas, over time creating wild populations (Alaska Natural Heritage Program 2006). Able to tolerate a wide range of climates and habitat types in its native Europe, EBC thrives in cold climates and wet soils, making it well suited for riparian zones in Alaska (Leather 1996). EBC has spread rapidly in the last ten years, and appears to be displacing native trees in riparian forests along streams in parts of urban Alaska (Flagstad et al. 2010). EBC is able to form dense, monotypic stands, and is ranked as *highly invasive* (Carlson et al. 2008).

While the rapid spread of EBC has been documented, basic ecological information is lacking (Flagstad et al. 2010). Little is known about the current distribution of EBC in Alaska, let alone what effect it may have on stream ecosystems, stream-riparian forest linkages, and associated ecological processes. This thesis investigates the effects of EBC colonization on stream-riparian interactions, natural ecological processes and on invertebrate prey resources for stream-rearing salmonids. This project is divided into three parts. In the first chapter I document the current distribution of EBC along two streams in Anchorage, Alaska: Campbell and Chester creeks. In the second chapter I examine the effects of EBC on the ecological processes of leaf litter break down and shredder colonization by conducting leaf pack experiments. In the third chapter I assess the effects of riparian EBC on terrestrial invertebrate prey resources for juvenile coho salmon (*Oncorhynchus kisutch*).

Collectively, the results of this work provide clues about the extent to which invasive riparian plants can affect native species and ecological processes in stream ecosystems of Alaska. These findings will ultimately help guide management of EBC by land management agencies involved in managing urban watersheds, fisheries, and controlling invasive species.

References

Abelho, M. and M.A.S. Graça. 1996. Effects of eucalyptus afforestation on leaf litter dynamics and macroinvertebrate community structure of streams in central Portugal. Hydrobiologia 324: 195-204.

Alaska Natural Heritage Program. 2006. Non-Native Species of Alaska: European Bird Cherry (*Prunus padus* L.). http://akweeds.uaa.alaska.edu.

Allan, J.D. 1978. Trout predation and the size composition of stream drift. Limnology and Oceanography 23: 1231-1237.

Allan, J.D., M.S. Wipfli, J.P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Canadian Journal of Fisheries and Aquatic Sciences 60: 309–320.

Allen, K.R. 1951. The Horokiwi stream: a study of a trout population. New Zealand Department of Fisheries Bulletin 10.

Bailey, J.K., J.A. Schweitzer and T.G. Whitham. 2001. Salt cedar negatively affects biodiversity of aquatic macroinvertebrates. Wetlands 21: 442-447.

Baxter, C.V., K.D. Fausch, M. Murakami, and P.L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology 85: 2656-2663.

Baxter, C.V., K.D. Fausch, and W.C. Saunders. 2005. Tangled webs: Reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50: 201–220.

Bilby, R. E. and J. W. Ward. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington. Canadian Journal of Fisheries & Aquatic Sciences 48: 2499-2508.

Braatne, J.H., S.M.P. Sullivan and E. Chamberlain. 2007. Leaf decomposition and stream macroinvertebrate colonization of Japanese knotweed, an invasive plant species. International Review of Hydrobiology 92: 656-665.

Canhoto, C. and M.A.S. Graça. 1995. Food value of introduced eucalypt leaves for a Mediterranean stream detritivore – *Tipula lateralis*. Freshwater Biology 34: 209-214.

Carlson, M.L. and M. Shephard. 2007. The spread of invasive exotic plants in Alaska: is establishment of exotics accelerating? In: Harrington TB, Reichard SH (eds) Meeting the challenge: invasive plants in Pacific northwestern ecosystems. USDA Forest Service PNW Research Station, Portland, pp 111–127.

Carlson, M.L., I.V. Lapina, M. Shephard, J.S. Conn, R. Densmore, P. Spencer, J. Heys, J. Riley, and J. Nielsen. 2008. Invasiveness ranking system for non-native plants of Alaska. USDA Forest Service, R10, R10-TP-143, p 218.

Cummins, K.W., M.A. Wilzbach, D.M. Gates, J.B. Perry, and W.B. Taliaferro. 1989. Shredders and riparian vegetation: leaf litter that falls into streams influences communities of stream invertebrates. BioScience 39: 24-30.

Dangles, O., M. Jonsson, and B. Malmqvist. 2003. The importance of detritivore species diversity for maintaining stream ecosystem functioning following the invasion of a riparian plant. Biological Invasions 4: 441-446.

Dukes, J.S. and H.A. Mooney. 1999. Does global change increase the success of biological invaders? Trends in Ecology and Evolution 14: 135-139.

Edwards, E. D. and A.D. Huryn. 1995. Annual contribution of terrestrial invertebrates to a New Zealand trout stream. New Zealand Journal of Marine and Freshwater Research 29:467-477.

Flagstad, L.A., H. Cortés-Burns and T.L. Roberts. 2010. Invasive plant inventory and bird cherry control trials phase II: bird cherry distribution, demography, and reproduction biology along Chester and Campbell Creek trails, Anchorage, Alaska. Alaska Natural Heritage Program, p. 61.

Friedman, J.M., G.T. Auble, P.B. Shafroth, M.L. Scott, M.F. Merigilano, M.D. Preehling and E.K. Griffith. 2005. Dominance of non-native riparian trees in western USA. Biological Invasions 7: 747-751.

Gerber, E., C. Krebs, C. Murrell, M. Moretti, R. Rocklin and U. Scnaffner. 2008. Exotic invasive knotweeds (*Fallopia spp*.) negatively affect native plant and invertebrate assemblages in European riparian habitats. Biological Conservation 141: 646-654.

Gessner, M.O. and E. Chauvet. 2002. A case for using litter breakdown to assess functional stream integrity. Ecology 12: 498-510.

Giannico, G.R. and M.C. Healey. 1999. Ideal free distribution theory as a tool to examine juvenile coho salmon (*Oncorhynchus kisutch*) habitat choice under different conditions of food abundance and cover. Canadian Journal of Fisheries and Aquatic Sciences 56: 2362-2373.

Glova, G. and P. Sagar. 1994. Comparison of fish and macroinvertebrate standing stocks in relation to riparian willows (*Salix* spp.) in three New Zealand streams. New Zealand Journal of Marine and Freshwater Research 28: 255-266.

Going, B.M. and T.L. Dudley. 2008. Invasive riparian plant litter alters aquatic insect growth. Biological Invasions 10: 1041-1051.

Graça, M.A.S. 2001. The role of invertebrates on leaf litter decomposition in streams – a review. International Review of Hydrobiology 86: 383 – 393.

Greenwood, H., D.J. O’Dowd and P. S. Lake. 2004. Willow (*Salix rubens*) invasion of the riparian zone in south-eastern Australia: reduced abundance and altered composition of terrestrial arthropods. Diversity and Distributions 10: 485–492.

Gregory, S.V., F.J. Swanson, W.A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41: 540-551.

Herrera, A.M. and T.L. Dudley. 2003. Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (*Arundo donax*) invasion. Biological Invasions 5: 167-177.

Hierro, J.L. and R.M. Callaway. 2003. Allelopathy and exotic plant invasion: from molecules and genes to species interactions. Plant and Soil. 256: 29 - 39.

Hood, W.G. and R.J. Naiman. 2000. Vulnerability of riparian zones to exotic vascular plants. Plant Ecology 148: 105-114.

Irons, J.G., M.W. Oswood and J.P Bryant. 1988. Consumption of leaf detritus by a stream shredder – influence of tree species and nutrient status. Hydrobiologia 160: 53-61.

Johnson, J.H. and N.H. Ringler. 1980. Diets of juvenile coho salmon *(Oncorhynchus kisutch)* and steelhead trout *(Salmo gairdneri)* relative to prey availability. Canadian Journal of Zoology 58: 553-558.

Kawaguchi, Y. and S. Nakano. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. Freshwater Biology 43: 303-316.

Kawaguchi, Y., Y. Taniguchi, and S. Nakano. 2003. Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. Ecology 84: 701-708.

Kennedy, T.A. and S.E. Hobbie. 2004. Saltcedar (*Tamarix ramosissima*) invasion alters organic matter dynamics in a desert stream. Freshwater Biology 49: 65-76.

Kennedy, T.A., J.C. Finlay, and S.E. Hobbie. 2005. Eradication of invasive *Tamarix ramosissima* along a desert stream increases native fish density. Ecological Applications. 15: 2072 – 2083.

Lacan, I., V.H. Resh, and J.R. McBride. 2010. Similar breakdown rates and benthic macroinvertebrate assemblages on native and *Eucalyptus globulus* leaf litter in Californian streams. Freshwater Biology 55: 739-752.

Leather, S.R. 1996. *Prunus padus* L. Journal of Ecology 84: 125-132.

Lecerf, A., M. Dobson, C.K. Dang and E. Chauvet. 2005. Riparian plant species loss alters trophic dynamics in detritus-based stream ecosystems. Oecologia 146: 432-442.

Lecerf, A., D. Patfield, A. Boiche, M.P. Riipinen, E. Chauvet, and M. Dobson. 2007. Stream ecosystems respond to riparian invasion by Japanese knotweed (*Fallopia japonica*). Canadian Journal of Fisheries and Aquatic Sciences 64: 1273-1283.

Mason, C.F. and S.M. MacDonald, 1982. The input of terrestrial invertebrates from tree canopies to a stream. Freshwater Biology 4: 305 -311.

Meehan, W.R. 1996. Influence of riparian canopy on macroinvertebrate composition and food habits of juvenile salmonids in several Oregon streams. Res. Pap. PNW-RP-496. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 14 p.

Moline, A.B. and N.L. Poff. 2008. Growth of an invertebrate shredder on native (*Populus*) and non-native (*Tamarix*, *Elaeagnus*) leaf litter. Freshwater Biology 53: 1012-1020.

Motomori, K., H. Mitsuhashi, and S. Nakano. 2001. Influence of leaf litter quality on the colonization and consumption of stream invertebrate shredders. Ecological Research 16: 173-182.

Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. Nature 368:734–736.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999a. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80: 2435-2441.

Nakano, S., Y. Kawaguchi, Y. Taniguchi, H. Miyasaka, Y. Shibata, H. Urabe, and N. Kuhara. 1999b. Selective foraging on terrestrial invertebrates by rainbow trout in forested headwater stream in northern Japan. Ecological Research 14: 351-360.

Nakano, S. and M. Murakami. 2001. Dynamic interdependence between terrestrial and aquatic food webs. Proceedings in National Academy of Sciences 98: 166-170.

Ober, H.K. and J.P. Hayes. 2008. Influence of forest riparian vegetation on abundance and biomass of nocturnal flying insects. Forest Ecology and Management 256: 1124-1132.

Peterson, R.C. and K.W. Cummins. 1974. Processing in a woodland stream. Freshwater Biology 4: 345-368.

Piccolo, J.J. and M.S. Wipfli. 2002. Does red alder (*Alnus rubra*) in upland riparian forests elevate macroinvertebrate and detritus export to downstream habitats in southeastern Alaska? Canadian Journal of Fisheries and Aquatic Sciences 59: 503-513.

Planty-Tabacchi, A.M., E. Tabacchi, R.J. Naiman, C. Deferrari, and H. Décamps. 1996. Invasibility of species-rich communities in riparian zones. Conservation Biology 10: 598–607.

Read, M.G. and L.A. Barmuta. 1999. Comparisons of benthic communities adjacent to riparian native eucalypt and introduced willow vegetation. Freshwater Biology 42: 359-374.

Romero, N., R.E. Gresswell and J.L. Li. 2005. Changing patterns in coastal cutthroat trout (*Oncorhynchus clarki clarki*) diet and prey in a gradient of deciduous canopies. Canadian Journal of Fisheries and Aquatic Sciences 62: 1797-1807.

Sampaio, A., R. Cortes and C. Leao. 2001. Invertebrate and microbial colonization in native and exotic leaf litter species in a mountain stream. International Review of Hydrobiology 86: 527-540.

Sanderson, B.L., K.A. Barnas and A.M. Rub. 2009. Nonindigenous species of the Pacific Northwest: An overlooked risk for endangered salmon? BioScience 59: 245 -256.

Schowalter, T.D., W.W. Hargrove, and D.A. Crossley Jr. 1986. Herbivory in forested ecosystems. Annual Review of Entomology 31: 177–196.

Swan, C.M., B. Healey and D.C. Richardson. 2008. The role of native riparian tree species in decomposition of invasive tree of heaven (*Ailanthus altissima*) leaf litter in an urban stream. Ecoscience 15: 27-35.

Tabacchi, E., D. L. Correll, R. Hauer, G. Pinay, A.M. Planty-Tabacchi, and R. C. Wissmar. 1998. Development, maintenance and role of riparian vegetation in the river landscape. Freshwater Biology 40: 497-516.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.

Wallace, J.B., S.L. Eggert, J.L. Meyer, and J.R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277: 102-104.

Webster, J.R. and E.F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics 17: 567–594.

Wiesenborn, W.D. 2005. Biomass of arthropod trophic levels on *Tamarix ramosissima* (Tamaricaceae) branches. Environmental Entomology 34: 656-663.

Wilcove, D.S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48: 607-615.

Wipfli, M.S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. Canadian Journal of Fisheries and Aquatic Sciences 54: 1259-1269.

Wipfli, M.S. and D.P. Gregovich. 2002. Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. Freshwater Biology 47: 957–969.

Wipfli, M.S. and C.V. Baxter. 2010. Linking ecosystems, food webs, and fish production: Subsidies in salmonid watersheds. Fisheries 35: 373-387.

Chapter 1

The abundance and distribution of invasive *Prunus* spp. in riparian forests along streams in Anchorage, Alaska[1]

Abstract

Invasive species are a concern worldwide because they are able to displace native species and reduce biodiversity. European bird cherry (*Prunus padus*) is a non-native ornamental tree that is spreading rapidly and possibly displacing native trees in riparian forests along streams in parts of urban Alaska. Yet there has been little effort to map its distribution and understand its ecological effects. We surveyed riparian vegetation along streams in two watersheds in Anchorage, Alaska, Campbell and Chester creeks, where *P. padus* has colonized and appears to be spreading. Our surveys found *P. padus* to be widespread along these streams occurring in 40% of plots along Campbell Creek and 55% of plots along Chester Creek. *P. padus* was abundant within the ground cover as seedlings, in the understory as saplings, and occurred as mature trees within forest canopies. Distribution maps show riparian forests closer to the city center contained more mature plants while mostly younger plants composed habitats further upstream. We also documented a second species of ornamental cherry (*Prunus virginiana*) growing along these streams. Collectively, these data will help guide management of invasive *Prunus* species in Alaska by providing a baseline inventory as they continue to spread over time.

---

[1] Roon, D.A., M.S. Wipfli, T.L. Wurtz and A. Prakash. The abundance and distribution of invasive *Prunus* spp. in riparian forests along streams in Anchorage, Alaska. Prepared for submission to Biological Invasions.

Introduction

The spread of invasive plant species is a concern worldwide because they can cause serious ecological effects - displacing native species, reducing biodiversity, and disrupting ecological processes (Hood and Naiman 2000, Sher et al. 2002, Friedman et al. 2005, Ringold et al. 2008). Riparian zones can support a higher percentage of invasive plants than upland habitats due to the combined effects of flood events that disturb riparian soils and landscape connectivity linking populations along riparian corridors (Planty-Tabacchi et al. 1996, Hood and Naiman 2000). As a result, invasive plants in riparian forests are spreading in many locations throughout the world, with notable invasions of tamarisk (*Tamarix* spp.) in the western United States; eucalyptus (*Eucalyptus* spp.) and knotweeds (*Fallopia* spp.) in Europe; and willows (*Salix* spp.) in Australia (Hood and Naiman 2000, Sher et al. 2002, Friedman et al. 2005, Ringold et al. 2008). Alaskan habitats have been considered to be relatively unaffected by invasive species due to the state's geographic isolation. However, recent research has documented invasive plants are spreading from urban centers in Alaska into adjacent natural habitats (Carlson and Shephard 2007).

European bird cherry (*Prunus padus*) is a non-native deciduous tree that is spreading rapidly and possibly displacing native trees in riparian forests along streams in parts of urban Alaska (Flagstad et al. 2010). Able to tolerate a wide range of climates and habitat types in its native Europe, *P. padus* thrives in cold climates and wet soils, making it well suited for riparian zones in Alaska (Leather 1996). Also known as Mayday tree and choke cherry, it is frequently planted in Alaska as an ornamental species for its showy floral display (Alaska Natural Heritage Program 2006). Birds feed on the cherries and disperse the seeds from source trees to adjacent natural areas, creating wild populations over time (Alaska Natural Heritage Program 2006). *P. padus* has spread rapidly in the last 10 years, and appears to be displacing native trees in riparian forests along streams in parts of urban Alaska (Flagstad et al. 2010). *P. padus* is able to form dense, monotypic stands, and among invasive plant species in Alaska it is ranked as ‘highly invasive’ (Carlson et al. 2008).While the rapid spread of *P. padus* in riparian forests has been observed, the distribution has not been documented in Alaska.

The objectives of this study were to document the distribution and abundance of *P. padus* along two streams located within the Municipality of Anchorage, Campbell and Chester creeks, where this plant is well established, and appears to be spreading. These data will provide baseline information for land managers to document its current population and understand its future spread.

Study Site

This study focused on two Anchorage streams, Campbell and Chester creeks. Chester Creek is a smaller, more urbanized watershed, covering 78 km^2 while Campbell Creek is larger, less urbanized watershed covering 202 km^2 (Ourso and Frenzel 2003). Located in the southcentral part of Alaska (61º 10’ N, 149º 45’ W), Anchorage is characterized by a coastal climate considered to be a transitional zone between boreal and temperate rainforest biomes (Milner and Oswood 2000). Originating in the Chugach Mountains, these streams flow west through the urbanized lowlands of the Anchorage bowl before ultimately reaching the saltwater of Cook Inlet. Greenbelt corridors of municipal parkland parallel the lower portions of both streams, keeping the riparian zones largely intact as they flow through Alaska’s largest city (Ourso and Frenzel 2003). Both streams support wild populations of Pacific salmon (*Oncorhynchus* spp.) that provide valuable recreational fisheries for local residents.

Riparian vegetation is composed of mixed coniferous and deciduous forests dominated by spruce (*Picea* spp.), black cottonwood (*Populus trichocarpa*), paper birch (*Betula neoalaskana*), alder (*Alnus* spp.), and willow (*Salix* spp.). EBC is widespread along the lower, urbanized portions of these watersheds, completely displacing native riparian vegetation in places (Flagstad et al. 2010).

Methods

To determine the distribution of *P. padus* along Campbell and Chester creeks, we surveyed riparian vegetation following the methods outlined by the Alaska Natural Heritage Program (Flagstad et al. 2010). Starting at the mouth of each creek, riparian vegetation was surveyed systematically every 200 m. We established 5 × 5 m plots (25 m^2) on both banks of the stream channel at 133 locations on Chester Creek (*n* = 265 total plots) in 2009 and 171 locations on Campbell Creek (*n* = 342 total plots) in 2010. Within each plot, all woody tree species were identified, number of stems counted and percent cover estimated. All the vegetation data were averaged to calculate mean abundance – by percent cover and stem count. The surveys focused on the lower, urbanized portions of the watersheds where *P. padus* was predicted to be more abundant and continued upstream. While the riparian vegetation was intact along the majority of these creeks, we were unable to conduct the surveys in some locations because the streamside vegetation was absent due to urbanization.

P. padus occurrence and maturity in riparian forests were categorized by the following succession levels (Flagstad et al. 2010) as:

<u>0:</u> Completely native. No *P. padus* present.

<u>1:</u> Native dominant. At least one *P. padus* seedling present; seedlings comprising up to 10% of the understory; *P. padus* absent from the canopy.

<u>2:</u> Native less dominant. *P. padus* comprising 10 to 25% of understory; less than 10% *P. padus* in the canopy.

<u>3:</u> Mixed native-*Prunus*. *P. padus* comprising 25 to 50% of understory; *P. padus* comprising 10 to 25% of the canopy.

<u>4:</u> *Prunus* dominant. *P. padus* dominating understory (25-75%); many *P. padus* (25-50%) comprising the canopy.

<u>5:</u> *Prunus* monoculture. *P. padus* dominates the understory (> 75%) and canopy (> 50%).

GPS coordinates of each survey location were loaded into ArcGIS to map the spatial distribution of riparian *P. padus* along the study streams.

Results

Our surveys found *P. padus* to be widespread, occurring in 55% of the plots along Chester Creek and 40% of the plots along Campbell Creek (Table 1.3). *P. padus* appeared to be very abundant in the understory of riparian forests of both streams. Along Chester Creek, *P. padus* was the most abundant understory species by percent cover and stem count, covering a mean of 11.4% of the plot and a mean of 78.4 stems per plot (Table 1.1). *P. padus* was the third most abundant understory species by percent cover after alder and willow, accounting for a mean of 2.9% cover, along Campbell Creek. However, *P. padus* was the most abundant species by stem count, with a mean of 16.8 stems per plot (Table 1.2). A similar pattern of *P. padus* dominance in the understory appeared when the plot succession levels were considered. Plots where the *P. padus* infestation was limited primarily to the understory (Levels 1 and 2) accounted for 41.5% of plots along Chester Creek and 33.9% of plots along Campbell Creek (Table 1.3).

Native riparian tree species dominated the canopy of riparian forests along both creeks. Alaska paper birch and cottonwood dominated the canopy of plots along Chester Creek, while alder, spruce and birch dominated the canopy of plots along Campbell Creek (Tables 1.1 & 1.2). *P. padus* accounted for 9.3% and 3.4% of the canopy cover of plots along Chester Creek and Campbell Creek, respectively (Tables 1.1 & 1.2). Succession levels showed *P. padus* populations were present in the canopy, but occurred less frequently than in the understory (Levels 3 and 4), only composing 12.8% of plots surveyed along Chester Creek and 4.7% of plots along Campbell Creek. Although rare, we observed dense monotypic stands of *P. padus* (Level 5), where native trees were locally displaced. These occurred in 12 plots (4.5%) along Chester Creek and 5 plots (1.5 %) along Campbell Creek (Table 1.3).

Distribution maps show a semicontinuous distribution of *P. padus* along the lower portions of the Campbell and Chester creek watersheds that becomes more sporadic heading upstream (Fig. 1.1). *P. padus* was more frequent in the urbanized extent of the watershed and occurred less often in the less urbanized habitats. Maps also showed that *P. padus* infestations were successionally more mature in the more urbanized portion of the watershed, and if present, occurred in earlier successional stages further upstream, away from the urban center (Fig. 1.1).

Our surveys documented a second species of ornamental cherry, *Prunus virginiana*, also known as Canadian red cherry or chokecherry, growing along these streams. Much less common than *P. padus*, we observed *P. virginiana* in a total of 35 plots (13.2%) along Chester Creek and 6 plots (2%) along Campbell Creek (Table 1.4). Most abundant in the understory, *P. virginiana* accounted for 0.3% cover and 0.7 stems of the understory per plot along Chester Creek and less than 0.1% cover and 0.1 stems of the understory per plot along Campbell Creek (Tables 1.1 & 1.2). *P. virginiana* was distributed more sporadically than *P. padus*, occurring almost exclusively in the urbanized portion of both watersheds (Fig. 1.2).

Discussion

Our surveys documented *P. padus* to be widespread along Campbell and Chester creeks. Percent cover, stem count, and succession level data show the current population of *P. padus* was mostly limited to the understory of riparian forests, composed of seedlings and saplings. Riparian forest canopies appeared to be dominated largely by a mix of native spruce, alder, birch, and cottonwood – with *P. padus* present, but occurring less frequently. However, in a few areas we found *P. padus* had sufficient time to locally displace native species, forming a dense monotypic stand. These patterns suggest that while the current population of *P. padus* is young, occurring mostly in the understory, stands are maturing and occupying the canopies in places, and could completely displace native species over time.

Two factors should be considered in understanding how the community composition of these riparian forests may change over time. First, our stem count data show that *P padus* seedlings outnumbered native seedlings dramatically, supporting a mean of 16.8 seedlings per plot along Campbell Creek and 78.4 seedlings per plot along Chester Creek. Not only could *P. padus* displace native species as it matures and moves into the canopy of riparian forests, but it could also reduce the recruitment of native seedlings. Nothing is known about the competitive mechanisms that are responsible for this pattern, but many invasive species harbor strong secondary compounds used to outcompete native species (Hierro and Callaway 2003). Known to produce cyanogenic glycosides, allelopathy could explain *P. padus'* ability to outcompete native species and decrease recruitment of native seedlings (Leather 1996, Hierro and Callaway 2003).

Second, the dominant native riparian plant species in coastal Alaska, thin-leaf alder (*Alnus tenuifolia*), has been decreasing in cover across southcentral Alaska from the combined effects of a canker and introduced insect pests responsible for defoliating the branches (Ruess et al. 2009). Important ecologically as a nitrogen fixer, a decrease in riparian alder cover could open up niches along stream banks, facilitating the germination and establishment of *P. padus* (Orlikowska et al. 2004). A shift from alder to *P. padus* could have ecological consequences, possibly affecting nutrient content and cycling of stream and riparian ecosystems (Orlikowska et al. 2004). Research has already documented some ecological consequences associated with riparian *P. padus*, finding that it may be negatively affecting invertebrate prey communities for stream-rearing salmonids in these watersheds (see Chapter 3). The ecological effects highlighted by this study could be accentuated if *P. padus* continues to spread these watersheds.

Our distribution maps show that the current population of *P. padus* is mostly within the residential and urbanized extent of the Campbell and Chester creek watersheds. Not only did it occur more frequently in these areas, but these populations appeared to be older, characterized by higher succession classes in these areas. *P. padus* also appears to be moving into the more pristine upstream portion of both watersheds. Populations in these locations were younger and most frequently characterized by seedlings. This pattern is highlighted by differences between watersheds. We documented *P. padus* to be more abundant in the more urbanized, Chester Creek watershed than the more pristine, Campbell Creek watershed. We also observed that the second species of ornamental cherry, *P. virginiana*, occurred entirely within the urban extent of each watershed and was more abundant along Chester Creek than Campbell Creek. Over time, *P. virginiana* may follow a pattern similar to *P. padus*, spreading beyond the urbanized extent and become established into more pristine areas.

Several mechanisms of spread that are potentially at work could explain the current distribution and help predict the future spread of *P. padus* in these watersheds. First, land use is an important factor, with *P. padus* occurring more frequently in areas that have been disturbed through urbanization and residential development. Residential areas appear to support the highest abundance and maturity *P. padus* populations, especially evident in the more-urbanized Chester Creek watershed. This could be because wild populations have established directly from trees planted in yards adjacent to stream channels, or indirectly established from birds feeding on fruits and defecating seeds along streams. Birds are thought to be the primary vector responsible for dispersing cherries. The spread of a second species of ornamental cherry (*P. virginiana*) along these streams further suggests that birds are a likely vector responsible and could spread other non-native fruit-bearing trees (Gosper and Vivian-Smith 2009). Finally, the streams themselves could be acting as a vector, carrying the buoyant cherries downstream where they eventually could wash up on shore, and germinate. It is difficult to say which dispersal mechanisms are most important, or how and if they interact, but they are all likely play a role in the spread of *Prunus* species. Based on the patterns of dispersal, areas susceptible to future spread include the upper reaches of these watersheds, other watersheds adjacent to the Municipality of Anchorage and others major urban or residential areas of Alaska.

In conclusion, we found the current invasion of *P. padus* along Campbell and Chester creeks was mostly in the understory of riparian forests located within the urbanized portions of these watersheds. We observed *P. padus* increasing in canopies, capable of locally displacing native species and spreading into less disturbed habitats. *P. virginiana*, a second species of ornamental cherry, also appears to be spreading along these streams, potentially following a similar trajectory but at an earlier successional stage. These data support the observation made by Carlson and Shephard (2007) that like other invasive plants in Alaska, while the current distribution of invasive *Prunus* species is largely limited to the urbanized portions of these watersheds, they are beginning to spread into adjacent natural habitats. These data in addition to complementary studies assessing the ecological effects associated with invasive *Prunus* species (Chapters 2 & 3) will help guide management of invasive *Prunus* species in Alaska by providing a baseline inventory as they continue to spread over time.

Acknowledgements

We thank Dustin Merrigan, John Hill, Steve Ewest, Rebecca Mierzejewski, Michael Rasy and Ashley West for assistance with field work. Thanks to Helen Cortés-Burns, Lindsey Flagstad and Matt Carlson at the Alaska Natural Heritage Program for assistance with developing the sampling protocol. This research was funded by the US Fish and Wildlife Service, USDA Forest Service, Alaska EPSCoR, and the Institute of Arctic Biology.

References

Alaska Natural Heritage Program (2006) Non-native species of Alaska: European Bird Cherry (*Prunus padus* L.). http://akweeds.uaa.alaska.edu.

Carlson ML and Shephard M (2007) The spread of invasive exotic plants in Alaska: is establishment of exotics accelerating? In: Harrington TB, Reichard SH (eds) Meeting the challenge: invasive plants in Pacific northwestern ecosystems. USDA Forest Service PNW Research Station, Portland, 111–127.

Carlson ML, Lapina IV, Shephard M, Conn, JS, Densmore R, Spencer P, Heys J, Riley J, and Nielsen J (2008) Invasiveness ranking system for non-native plants of Alaska. USDA Forest Service, R10, R10-TP-143, p 218.

Flagstad LA, Cortés-Burns H, and Roberts TL (2010) Invasive plant inventory and bird cherry control trials phase II: bird cherry distribution, demography, and reproduction biology along Chester and Campbell Creek trails, Anchorage, Alaska. Alaska Natural Heritage Program, p 61.

Friedman JM, Auble GT, Shafroth PB, Scott ML, Merigliano MF, Freehling MD and Griffin ER (2005) Dominance of non-native riparian trees in western USA. Biological Invasions 7: 747–751.

Gosper CR and Vivian-Smith G (2009) The role of fruit traits of bird-dispersed plants in invasiveness and weed risk assessment. Diversity and Distributions 15:1037-1046.

Hierro JL and Callaway RM (2003) Allelopathy and exotic plant invasion: from molecules and genes to species interactions. Plant and Soil 256: 29 - 39.

Hood WG and Naiman RJ (2000) Vulnerability of riparian zones to invasion by exotic vascular plants. Plant Ecology 148: 105-114.

Leather SR (1996) Biological flora of the British Isles: *Prunus padus* L. Journal of Ecology 84: 125-132.

Milner AM and Oswood MW (2000) Urbanization gradients in streams of Anchorage, Alaska: a comparison of multivariate and multimetric approaches to classification. Hydrobiologia 422: 209-223.

Orlikowska EH, Deal RL, Hennon PE and Wipfli MS (2004) The role of red alder in riparian forest structure along headwater streams in southeastern Alaska. Northwest Science 78: 111-123.

Ourso RT and Frenzel SA (2003) Identification of linear and threshold responses in streams along a gradient of urbanization in Anchorage, Alaska. Hydrobiologia 501: 117-131.

Planty-Tabbachi AM, Tabacci E, Naiman RJ, Defarri C and Decamps H (1996) Invasibility of species rich communities in riparian zones. Conservation Biology 10: 598-607.

Ringold PL, Magee TK and Peck DV (2008) Twelve invasive plant taxa in US western riparian ecosystems. Journal of North American Benthological Society 27: 949-966.

Ruess RW, McFarland JM, Trummer LM and Rohrs-Richey JK (2009) Disease-mediated declines in N-fixation inputs by *Alnus tenuifolia* to early-successional floodplains in Interior and South-Central Alaska. Ecosystems 12: 489-502.

Sher AA, Marshall DL and Taylor JP (2002) Establishment patterns of native *Populus* and *Salix* in the presence of invasive nonnative *Tamarix*. Ecological Applications 12: 760-772.

Table 1.1. Vegetation data from Chester Creek plots. Mean understory, canopy and total percent cover and stem count values for invasive *Prunus* spp. and native tree species in plots that were surveyed along the more urbanized Chester Creek in 2009 (*n* = 265).

	Understory		**Canopy**		**Total**	
Species	**% Cover**	**Count**	**% Cover**	**Count**	**% Cover**	**Count**
Picea spp.	1.4	1.4	7.3	1.3	8.7	2.7
Alnus spp.	1.9	2.1	6.7	1.1	8.6	3.2
Betula neoalaskana	0.9	1.5	24.8	2.0	25.7	3.5
Populus trichocarpa	1.0	2.6	21.5	1.6	22.5	4.3
Salix spp.	5.5	3.6	3.0	0.4	8.5	4.0
Total native species	**10.7**	**11.2**	**63.3**	**6.4**	**74.0**	**17.6**
Prunus padus	11.4	78.4	9.3	0.7	20.7	79.1
Prunus virginiana	0.3	0.7	0.0	0.0	0.3	0.7
Total *Prunus* species	**11.7**	**79.1**	**9.3**	**0.7**	**21.0**	**79.8**

Table 1.2. Vegetation data from Campbell Creek plots. Mean understory, canopy and total percent cover and stem count values for invasive *Prunus* spp. and native tree species in plots that were surveyed along the less urbanized Campbell Creek in 2010 (*n* = 342).

	Understory		**Canopy**		**Total**	
Species	**% Cover**	**Count**	**% Cover**	**Count**	**% Cover**	**Count**
Picea spp.	0.8	0.8	11.8	1.2	12.5	2.0
Alnus spp.	3.6	5.1	18.4	1.9	22.1	7.0
Betula neoalaskana	1.1	3.9	11.2	0.3	12.2	4.3
Populus trichocarpa	0.4	4.6	5.9	0.1	6.3	4.7
Salix spp.	5.5	1.0	0.7	<0.1	6.1	1.0
Total native species	**11.4**	**15.4**	**48.0**	**3.6**	**49.4**	**19.0**
Prunus padus	2.9	16.8	3.4	1.0	6.3	17.8
Prunus virginiana	<0.1	<0.1	<0.1	0.0	<0.1	<0.1
Total *Prunus* species	**3.0**	**16.9**	**3.5**	**1.0**	**6.4**	**17.9**

Table 1.3. *Prunus* succession levels along Chester and Campbell creeks. The total number of plots that were surveyed per succession level for *Prunus padus* and *Prunus virginiana* in the more urbanized Chester Creek and less urbanized Campbell Creek.

		Succession Level						
Species	**Watershed**	**0**	**1**	**2**	**3**	**4**	**5**	**Total**
Prunus padus								
	Chester Creek	109	74	36	22	12	12	265
	Campbell Creek	205	96	20	9	7	5	342
Prunus virginiana								
	Chester Creek	230	33	2	0	0	0	265
	Campbell Creek	336	6	0	0	0	0	342

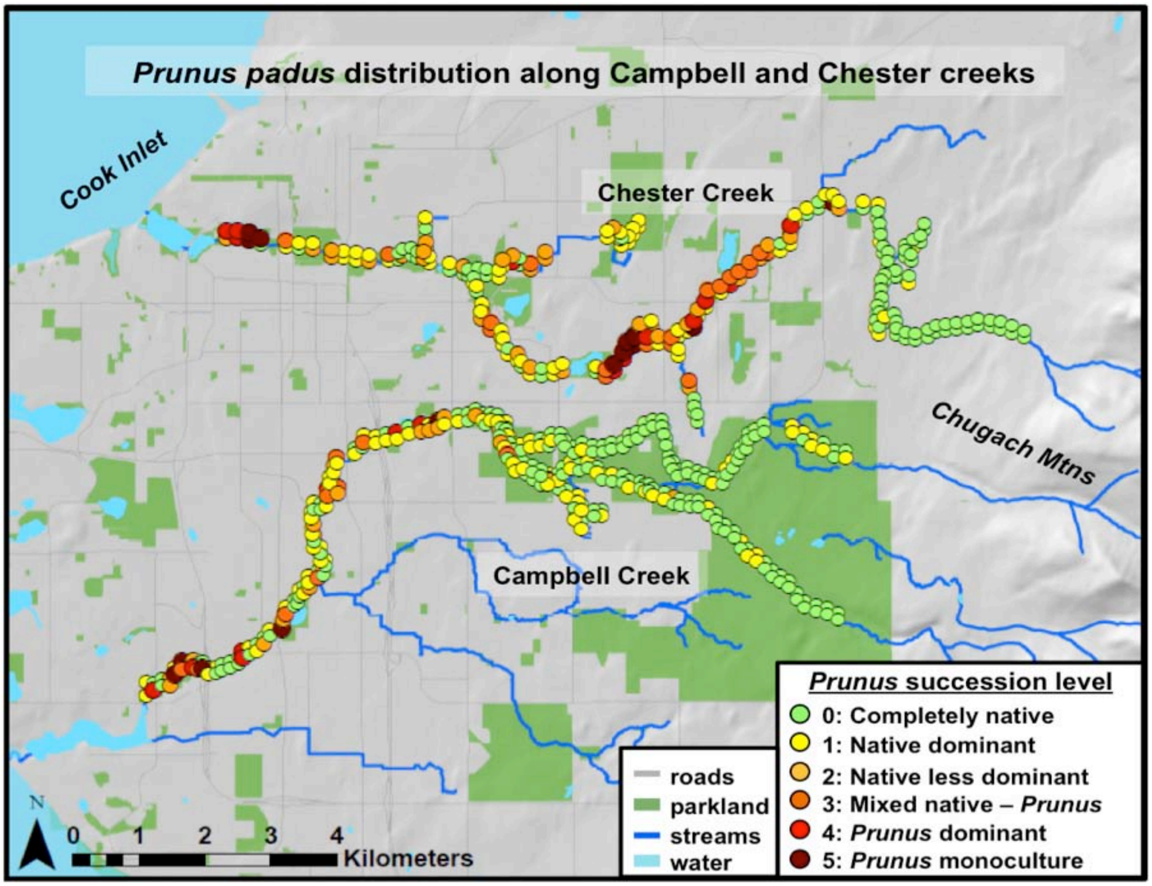

Fig. 1.1. Distribution of *Prunus padus* along Chester and Campbell creeks.

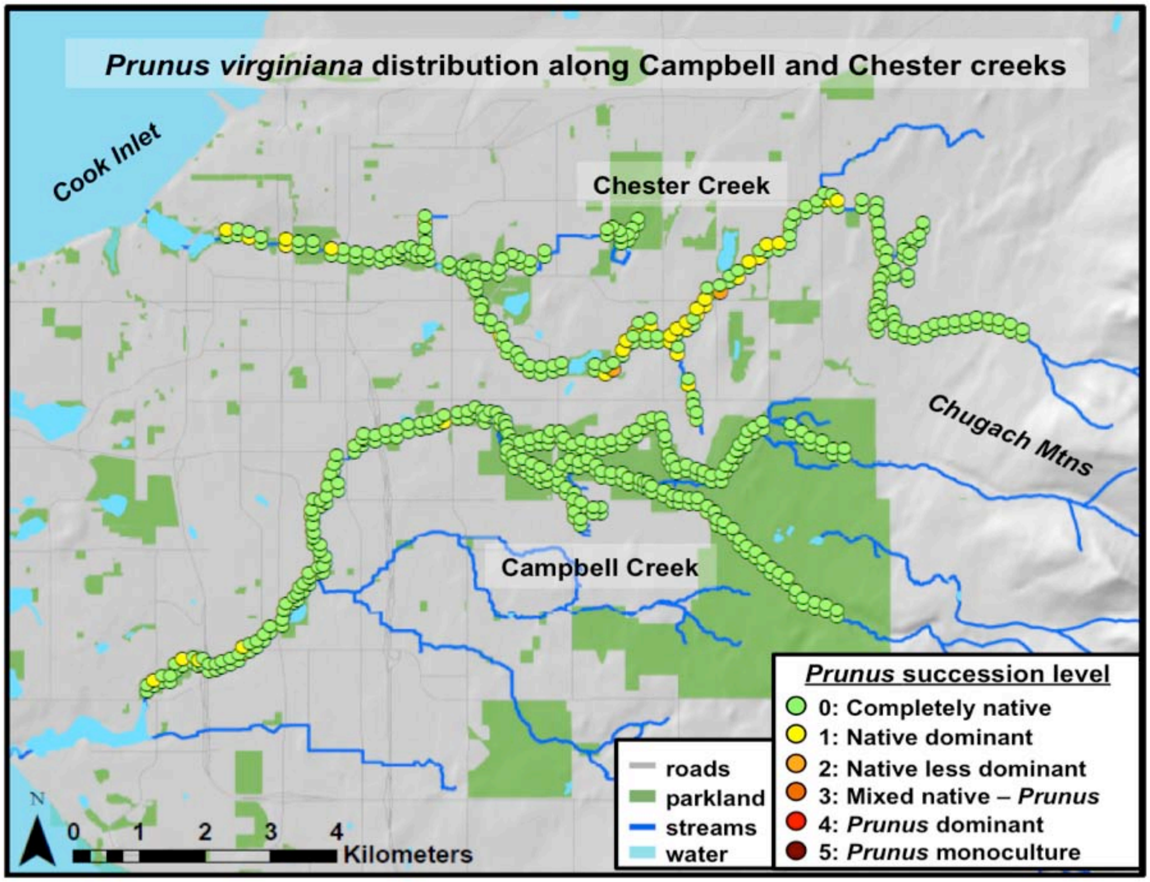

Fig. 1.2. Distribution of *Prunus virginiana* along Chester and Campbell creeks.

Chapter 2

Leaf litter processing is similar between native plants and invasive European bird cherry in urban Alaskan streams[1]

SUMMARY

1. Invasive species are a concern worldwide because they can displace native species, reduce biodiversity and disrupt ecological processes. Because riparian zones link terrestrial and aquatic ecosystems, the spread of invasive plants in riparian forests could affect stream-riparian interactions, stream food webs and ecosystem function.
2. European bird cherry (*Prunus padus*) (EBC) is an invasive ornamental tree that is spreading rapidly and possibly displacing native riparian trees along streams in parts of urban Alaska.
3. To determine how riparian EBC affects leaf litter processing by aquatic invertebrate shredders, we conducted leaf pack experiments in two Anchorage, Alaska streams - Campbell and Chester creeks. The first experiment contrasted invasive EBC with three native tree species – thin-leaf alder (*Alnus tenuifolia*), paper birch (*Betula neoalaskana*) and black cottonwood (*Populus trichocarpa*) - at a single site in Chester Creek, while the second experiment contrasted EBC with native alder at four sites in Campbell and Chester creeks.
4. In 2009, EBC leaf litter broke down significantly faster than that of the three native species. In 2010, while EBC leaf litter broke down significantly faster than alder in two locations in Chester Creek, EBC leaf litter broke down at a similar rate to alder in two locations in Campbell Creek.
5. EBC leaf litter supported similar aquatic invertebrate shredder communities compared to the leaf litter of native species in both experiments. Shredders did not differ

---

[1] Roon, D.A., M.S. Wipfli, and T.L.Wurtz. Leaf litter processing is similar between native plants and invasive European bird cherry in urban Alaskan streams. Prepared for submission to Freshwater Biology.

significantly by abundance or biomass, were similar in community structure and grew at similar levels between EBC and native species. Collectively, these results indicated that shredders utilized EBC leaf litter as a food source similarly to that of the native plant species.

6. While the spread of EBC in riparian forests may change the composition of leaf litter inputs into Alaska streams, our data show that leaf litter processing by aquatic invertebrate shredders was functionally similar between native plants and invasive EBC, not disrupting this ecological process in these streams.

Introduction

The spread of invasive plant species are a concern worldwide because they can displace native species, reduce biodiversity and disrupt ecological processes (Blossey, 1999; Mack *et al*., 2000; Dukes & Mooney, 2004). Riparian zones can support a higher percentage of invasive plants than upland habitats due to the combined effects of flood events that disturb riparian soils and landscape connectivity linking populations along riparian corridors (Planty-Tabacchi *et al*., 1996; Hood & Naiman, 2000). As a result, invasive plants in riparian forests are spreading in many locations, with notable invasions of Russian olive (*Elaeagnus angustifolia)* and tamarisk (*Tamarix* spp.) in the western United States; eucalyptus (*Eucalyptus* spp.) and knotweeds (*Fallopia* spp.) in Europe; and willows (*Salix* spp.) in Australia (Abelho & Graça, 1996; Blossey, 1999; Royer *et al*., 1999; Sher *et al*., 2002; Friedman *et al*., 2005; Lecerf *et al*., 2007). Because riparian zones link terrestrial and aquatic ecosystems, the spread of invasive plants in riparian forests could affect stream organisms, food webs and ecosystem function (Gregory *et al*., 1991; Hood & Naiman, 2000; Gessner & Chauvet, 2002).

One pathway through which invasive riparian plants can affect stream ecosystems is by changing the composition of allochthonous leaf litter inputs to streams. Low-order streams often rely on leaf litter inputs as basal energetic resources (Vannote *et al*., 1980; Webster & Benfield, 1986; Wallace *et al*., 1997). Aquatic invertebrate shredders feed on leaf litter inputs and process them into smaller fragments for other functional feeding groups (Vannote *et al*., 1980; Cummins *et al*., 1989; Wallace *et al*., 1997). If an invasive plant differs in quality from native species, for example through lower nutrient content, increased leaf toughness or presence of secondary plant compounds, it may affect shredder feeding activity and litter processing (Irons *et al*., 1988; Cummins *et al*., 1989; Abelho & Graça, 1996; Motomori *et al*., 2001). Previous studies have documented that invasive species in riparian zones can affect shredder biodiversity, abundance, community structure and growth (Abelho & Graça, 1996; Bailey *et al*., 2001; Dangles *et al*., 2003; Lecerf *et al*., 2007; Going & Dudley, 2008; Moline & Poff, 2008).

Because shredders process leaf litter inputs for other functional feeding groups of aquatic invertebrates, they have an important functional role in streams supporting upper trophic level consumers like stream fishes (Wallace *et al*., 1997; Baxter *et al*., 2005). If invasive species negatively affect shredder communities, effects could be expressed through multiple trophic levels, and disrupt ecological processes and functional integrity of streams (Cummins *et al*., 1989; Gessner & Chauvet, 2002; Baxter *et al*., 2005).

European bird cherry (*Prunus padus*) (EBC) is a non-native ornamental tree frequently planted in Alaska for its showy floral display (Alaska Natural Heritage Program, 2006). Birds feed on the cherries and disperse the seeds from source trees to adjacent natural areas, creating wild populations over time (Alaska Natural Heritage Program, 2006). Able to tolerate a wide range of climates and habitat types in its native Europe, EBC thrives in cold climates and wet soils, making it well suited for riparian zones in Alaska (Leather, 1996). EBC has spread rapidly in the last 10 years in Alaska, and appears to be displacing native trees in riparian forests along streams in parts of urban Alaska (Flagstad *et al*., 2010). EBC is able to form dense, monotypic stands and among invasive plant species in Alaska is ranked as “highly invasive” (Carlson *et al*., 2008).

At the same time, the dominant riparian tree species, thin-leaf alder (*Alnus tenuifolia*), appears to be decreasing across southcentral Alaska due to the combined effects of a canker and invasive insect pests that defoliate it (Ruess *et al*., 2009). As a nitrogen fixer, alder is an important source of nitrogen for riparian and stream ecosystems (Helfield & Naiman, 2002) and is a desirable food source for aquatic invertebrate shredders (Irons *et al*., 1988; Motomori *et al*., 2001). This shift in riparian vegetation from alder to EBC could have dramatic effects on stream food webs by changing the composition and quality of leaf litter inputs entering streams where this tree has colonized.

To determine if EBC affects leaf litter processing by aquatic invertebrate shredders in Alaska streams, the objectives of this study were to: 1) contrast leaf litter breakdown rates between EBC and native plants in selected urban Alaska streams, and 2) compare shredder communities associated with EBC leaf litter and that of native tree species. Based on previous studies looking at *Prunus* leaf litter, we hypothesized that EBC would break down faster than native species (Collen, 1994; Grubbs & Cummins, 1994). We also hypothesized that because EBC is a novel resource in these streams and may differ in leaf quality, EBC would support fewer aquatic invertebrate shredders than native plants. These data will help us understand how EBC leaf litter is processed in streams relative to native plant species and to what extent aquatic invertebrate shredders utilize EBC leaf litter as a food source, and will provide insight into whether riparian EBC can disrupt certain ecological processes important in stream ecosystems.

Methods

Study area

This study focused on two streams in the Municipality of Anchorage, Campbell and Chester creeks, where EBC is abundant (Chapter 1). Located in the southcentral part of the state, Anchorage, Alaska is characterized by a coastal climate considered to be a transitional zone between boreal and temperate rainforest biomes (Milner & Oswood, 2000). Originating in the Chugach Mountains, these streams flow west through the urbanized lowlands of the Anchorage bowl before ultimately reaching the saltwater of Cook Inlet. Greenbelt corridors of municipal parkland parallel the lower portions of both streams, keeping the riparian zones largely intact as they flow through the city (Fig. 2.1) (Ourso & Frenzel, 2003). Chester Creek is a second-order stream covering 78 km^2 and Campbell Creek is a fourth-order stream covering 158 km^2 (Fig. 2.1). Riparian vegetation is composed of mixed coniferous and deciduous forests dominated by spruce (*Picea* spp.), black cottonwood (*Populus trichocarpa*), paper birch (*Betula neoalaskana*), alder (*Alnus* spp.), and willow. EBC is widespread along the lower, urbanized portions of these watersheds, completely displacing native riparian vegetation in places (Flagstad *et al*., 2010).

Study site characteristics

We measured selected physical habitat and stream chemistry parameters to characterize and describe the study sites. Total canopy cover and canopy composition were measured with a handheld densiometer. Discharge was calculated using monthly flow measurements taken at each study site with a flow meter (Flo-Mate 2000, Marsh-McBirney Inc., Hach, CO). Stream pH and conductivity were taken monthly with a Hanna combination meter® (Hanna Instruments, Woonsocket, RI). Stream temperature was measured hourly with StowAway Tidbit Temperature data loggers® (Onset Computer Corporation, Pocasset, MA) to calculate mean temperature and total degree days accumulated throughout the experiments.

Leaf pack experiments

We conducted leaf pack experiments to determine EBC leaf litter processing rates relative to leaf litter of native riparian tree species, following the procedure outlined by Benfield (1996). The autumn before the experiment, senesced leaf litter was collected after abscission, air dried and stored in paper bags in dark rooms. Shortly before the experiments commenced, we dried the leaves at 60 °C for 24 hours. We constructed leaf packs from 10 mm mesh bags (20 x 20 cm) filled with 4 g of senesced leaf litter from a single species. Leaf packs were deployed randomly in a riffle habitat of stream and tethered to the streambed. At each removal date, we removed random sets of leaf packs, stored them in Ziploc® bags and refrigerated them until processed in the lab. To quantify leaf mass loss due to handling, an extra set of "handling loss" packs followed this procedure but were not left in the stream over time.

We set up two complementary leaf pack experiments with slightly different designs. In 2009, to determine how EBC leaf litter compared to the leaf litter of the dominant native species, we deployed leaf packs of four species – EBC and three native species including thin-leaf alder, paper birch, and black cottonwood - in the Chester Creek "urbanized" site where EBC dominated the riparian forest canopy. Five replicate leaf packs of all four species were removed at four dates (after 2, 22, 43 and 63 days) for a total of 80 leaf packs. In 2010, leaf pack experiments were conducted in four locations. We did this to determine if patterns in 2009 were repeated at the different locations subject to different habitat conditions, such as possible differences in thermal and flow regimes, aquatic invertebrate communities, and degrees of urbanization. Leaf packs of EBC and native alder were deployed in four sites using the same site from 2009 in Chester Creek and three new sites - an additional site in Chester Creek and two in Campbell Creek. We deployed leaf packs in a downstream "urbanized" reach and upstream "reference" reach of each stream. Three replicate packs of two species were removed over four dates (after 2, 12, 27, 54 days) at four sites for a total of 96 packs.

Laboratory procedures

Once removed from the stream, leaf packs were processed immediately in the lab. Leaves were rinsed with water over a 250 μm sieve to remove sediment and aquatic invertebrates. Leaves were then dried in a drying oven for 24 hr at 60°C and ashed at 550°C to calculate ash free dry mass (AFDM). AFDM was subtracted from the AFDM of the handling loss packs to calculate percent mass loss over time.

All sediment and aquatic invertebrates collected in the 250 μm sieve were stored in 90% ethanol in Whirlpaks® (Nasco, Fort Atkinson, WI) until later processed in the lab. While other functional feeding groups of aquatic invertebrates colonized the leaf packs, we focused exclusively on shredding taxa (Merritt & Cummins, 1996). Aquatic invertebrate shredders were identified to family, enumerated and their length measured to estimate biomass using published length-weight regressions (Benke *et al.*, 1999).

Statistical analysis

To compare the rate of leaf litter breakdown between EBC and native riparian plants, we used an ANCOVA model where leaf species and time were used to predict breakdown rate. Leaf litter breakdown rates were determined using an exponential decay model: $W_t = W_0 \, e^{-kt}$, where W_0 is the initial AFDM (g), Wt is the final AFDM (g) at time t, and k is the decay coefficient (Peterson & Cummins, 1974; Benfield, 1996). We then solved for the breakdown rate (k) where k is equal to the slope coefficient of the line when comparing the natural log of % AFDM remaining over time. In 2009, we compared EBC to three native species at one site and in 2010 we compared EBC to alder at four sites. To account for differences in stream temperature between sites, we compared breakdown rates by day (number of days in stream) and by degree day (accumulated temperature above 0 °C during the experiment).

To compare differences in aquatic invertebrate shredders associated with EBC and native riparian plants, in 2009 we used a repeated measures ANOVA where leaf species and time were used to predict shredder abundance (number) and biomass. However, in 2010, to account for differences between sites and streams we used a repeated measures ANOVA modified with a nested design, where leaf packs were nested within sites and sites were nested within streams. Shredder abundance and biomass data violated assumptions of equal variance and normality so we applied a log (x +1) transformation. We compared the community structure of aquatic invertebrate shredders by mean abundance and biomass between EBC and native riparian plant species using a nonmetric multidimensional scaling (NMDS) ordination. To compare invertebrate growth with different leaf species (EBC vs. native), we made proxy observations measuring the percent change in shredder length (mm) of each taxa over the duration of each leaf pack experiment. All data were analyzed with the statistical program R (R Development Core Team, version 2.10.1).

Results

Study site characteristics

All sites with the exception of the Campbell Creek urbanized site were small streams less than 6 m in width, 1 $m^3 s^{-1}$ discharge and greater than 50% canopy cover. EBC was present in the canopy at three of the four study sites, being most abundant at the two urbanized sites along Campbell Creek and Chester Creek (Table 2.1). Study sites varied substantially by stream temperature, with the downstream, urbanized sites averaging a higher temperature and accumulating more degree days than the reference sites further upstream in both Campbell and Chester creeks (Tables 2.1 & 2.2).

Leaf litter breakdown

Leaf pack experiments showed that EBC and some native species leaf litter broke down at slightly different rates. In 2009, all four species broke down quickly in the Chester Creek urbanized site, losing over 50% of their initial mass within the first 23 days and 90% of their mass after 43 days of being placed in the stream (Fig. 2.2). When comparing breakdown rates (k) by day, there was a significant effect of leaf species and date (ANCOVA; leaf species: $F_{4,95} = 134.3$, $P < 0.001$; date: $F_{4,95} = 134.3$, $P < 0.001$). EBC leaf litter broke down significantly faster than all native species, including alder ($P = 0.045$), birch ($P = 0.005$) and cottonwood ($P < 0.001$) (Table 2.2). A similar pattern was seen when comparing breakdown rates (k) by degree day (ANCOVA; leaf species: $F_{4,95} = 137.3$, $P < 0.001$; date: $F_{4,95} = 137.3$, $P < 0.001$). EBC broke down significantly faster than all native species, including alder ($P = 0.044$), birch ($P = 0.005$) and cottonwood ($P < 0.001$) (Table 2.2).

In 2010, EBC leaf litter broke down faster than alder in all four sites in Campbell and Chester creeks (Fig. 2.3). When comparing breakdown rates k by day, EBC leaf litter broke down more quickly, ranging between 0.0377 to 0.0772 k day^{-1}, compared to alder, which ranged from 0.0267 and 0.0569 k day^{-1} (Table 2.2). Both alder and EBC leaf litter broke down fastest at the Chester Creek urbanized site (k day^{-1}), which had the highest average stream temperature and accumulated the most degree days. While the slowest breakdown rate (k day^{-1}) for alder leaf litter occurred at the site with the coolest temperatures, it did not for EBC. EBC leaf litter (0.0036 - 0.0081 k degree day^{-1}) also broke down faster than alder (0.0027 - 0.0044 k degree day^{-1}) when comparing breakdown rates by degree days (Table 2.2).

While time (by day or degree days) had a significant effect across all sites, there was no consistent effect of leaf litter species. EBC broke down significantly faster than alder by both day and degree days in the Chester Creek urbanized site (ANCOVA; day: $F_{2,27} = 91.2$, $P = 0.015$; degree day: $F_{2,27} = 95.5$, $P = 0.014$) and the Chester Creek reference site (ANCOVA; day: $F_{2,27} = 83.1$, $P = 0.008$; degree day: $F_{2,27} = 81.7$, $P = 0.009$) (Table 2.2). While EBC also broke down faster than alder in both sites in Campbell Creek, the differences were not significant in the urbanized site (ANCOVA; day: $F_{2,27} = 133.7$, $P = 0.089$; degree day: $F_{2,27} = 118.8$, $P = 0.106$) or the reference site (ANCOVA; day: $F_{2,27} = 59.8$, $P = 0.102$; degree day: $F_{2,27} = 54.7$, $P = 0.114$) (Table 2.2).

Aquatic invertebrate shredders

Aquatic invertebrate shredders were abundant in Campbell and Chester creeks, colonizing both EBC and native leaf litter. In 2009, limnephilid caddisflies (which included a combination of *Ecclisocosmoecus* spp., *Ecclisomyia* spp., *Hesperophylax* spp., *Onocosmoecus* spp. and *Psychoglypha* spp.) were the most abundant taxa accounting for more than 66% of shredder abundance and 90% of shredder biomass for all litter types except cottonwood (Table 2.3). Nemourid stoneflies (*Zapada* spp.) were the most abundant shredder by number associated with cottonwood leaf litter, accounting for 63% while only comprising between 23 - 32% of other litter types by number and less than 5% by biomass (Table 2.3). Tipulid craneflies (*Tipula* spp.) were also present but rare, only occurring on alder and birch litter (Table 2.3). In 2010, limnephilid caddisflies again were the dominant shredder taxa by number and biomass for alder and EBC at all sites except the Campbell Creek reference site where nemourid stoneflies dominated (Table 2.3).

Tipulid craneflies colonized both EBC and alder leaf litter in 2010 but did not account for much biomass (Table 2.3).

In 2009, alder and birch leaf litter supported the highest numbers of shredders and while shredder abundance varied significantly by date, there was no significant difference between EBC and native species or species x date interaction (repeated measures ANOVA; leaf species: $F_{3,64} = 0.9$, $P = 0.439$; date: $F_{3,64} = 20.1$, $P < 0.001$; species x date interaction: $F_{9,64} = 0.8$, $P = 0.597$) (Fig. 2.4a). Shredder biomass did not differ significantly between EBC and native species (repeated measures ANOVA; species: $F_{3,64} = 0.6$, $P = 0.641$) or by date ($F_{3,64} = 1.8$, $P = 0.179$) (Fig. 2.4b). Alder supported the highest overall biomass of shredders throughout the experiment, but this difference was not significantly greater than EBC ($P = 0.731$). Nor did shredder biomass differ significantly between EBC and birch ($P = 0.932$) or cottonwood ($P = 0.638$) (Fig. 2.4b).

In 2010, overall shredder abundance varied significantly by stream, date, sites nested within stream, but not by leaf species nested within site (nested repeated measures ANOVA: stream: $F_{1,73} = 17.1$, $P < 0.001$; date: $F_{3,73} = 25.5$, $P < 0.001$; sites nested within stream: $F_{2,73} = 8.4$, $P < 0.001$, leaf species nested within sites: $F_{4,73} = 2.3$, $P = 0.064$ (Fig. 2.5a). Shredder abundance on alder leaf litter deployed in the Chester Creek was higher and marginally significant relative to EBC ($P = 0.057$) (Fig. 2.5a). Otherwise, shredder abundance did not differ significantly by leaf species at the remaining sites (Chester Creek reference $P = 0.522$; Campbell Creek urbanized $P = 0.176$; Campbell Creek reference $P = 0.272$) (Fig. 2.5a). Shredder biomass varied significantly by date, sites nested within stream, but not by stream or leaf species nested within site (nested repeated measures ANOVA: date: $F_{3,73} = 22.6$, $P < 0.001$; sites nested within stream: $F_{2,73} = 22.3$, $P < 0.001$; stream: $F_{1,73} = 0.3$, $P =0.567$; or leaf species nested within site: $F_{4,73} =1.2$, $P = 0.299$) (Fig. 2.5b). Shredder biomass did not differ significantly between leaf species at sites in Campbell Creek (urbanized site $P = 0.296$; reference site $P = 0.141$) or in Chester Creek (urbanized site $P = 0.459$; reference site $P = 0.342$) (Fig. 2.5b).

Shredder community structure did not appear to differ between EBC and native riparian tree species. NMDS ordination plots showed no clear differences between EBC and native leaf species for shredder abundance or biomass (Fig. 2.6). Instead, shredder communities grouped more closely by stream and site than by species.

Shredder growth did not show any clear patterns between years or among leaf litter species (Table 2.4). In 2009, limnephilid caddisflies grew in length by 46% on birch and by 85% on cottonwood leaf litter but decreased in size by 23% on alder and 21% on EBC. Nemourid stoneflies grew on all leaf litter species with the greatest growth occurring with EBC leaf litter (43%) (Table 2.4). Tipulid craneflies only occurred on alder and birch leaf litter at one removal date so we were unable to calculate growth. In 2010, both limnephilid caddisflies (43% vs. 16%) and nemourid stoneflies (41% vs. 37%) grew more on EBC leaf litter than alder while tipulid craneflies grew more on alder than EBC (66% vs. 10%) (Table 2.4).

Discussion

We found EBC leaf litter broke down quickly in Anchorage streams. In 2009, EBC leaf litter broke down significantly faster than all native species (alder, birch and cottonwood) when deployed in the Chester Creek urbanized site. In 2010, while EBC leaf litter broke down significantly faster in the two sites in Chester Creek, the differences were not significant in the Campbell Creek sites. It is unclear why the streams differed in statistical significance, but it could be due to the increased flow in Campbell Creek, a fourth order stream. Because leaf litter breakdown is a combination of physical and biological processes, the increased flow may have heightened the physical abrasion that the leaf litter of both species was subjected to, possibly muting the biological factors responsible for the differences in breakdown rates seen in Chester Creek (Peterson & Cummins, 1974; Webster & Benfield, 1986).

These results partially support our hypothesis that EBC leaf litter would break down more quickly than the leaf litter of native species. Studies by Cummins *et al*.

(1989) and Grubbs and Cummins (1994) also documented *Prunus* leaf litter to break down quickly in streams and categorized *Prunus* species as ‘fast’ decomposers. A study by Collen (1994) found EBC leaf litter broke down faster than alder and birch leaves in Scottish streams. However, our results conflict with other studies examining leaf litter breakdown of invasive species in streams. These studies found that in some cases differences in leaf litter quality can negatively affect the microbial colonization and conditioning of leaf litter (Webster & Benfield, 1986; Graça, 2001; Lecerf *et al*., 2007). This resulted in slower breakdown rates relative to native species with invasive plants like eucalyptus, Japanese knotweed, and tamarisk (Abelho & Graça, 1996; Sampaio *et al*., 2001; Kennedy & Hobbie, 2004; Braatne *et al*., 2007; Lecerf *et al*., 2007; Going & Dudley, 2008).

In our study, EBC leaf litter broke down at a similar or faster rate than native species at all sites in both experiments. Although it is likely that EBC differed from native species in leaf chemistry, we observed no decrease in leaf litter breakdown rate. In this case, it could be that the physical structure of the leaf litter was more influential than leaf chemistry causing the thin EBC leaves to fragment more quickly than the thicker native species (Peterson & Cummins 1974; Webster & Benfield, 1986). As a result, we observed patterns more similar to the other *Prunus* studies than the studies examining other invasive species.

Aquatic invertebrate shredders utilized EBC leaf litter, colonizing leaf packs deployed in Campbell and Chester creeks. Conflicting with our hypothesis, EBC leaf litter appeared to support similar shredder communities relative to native species. We observed that shredders in EBC leaf packs did not differ significantly by abundance or biomass compared to the leaf packs of native species of leaf litter. A NMDS ordination found that shredder community structure was more likely to differ by site and stream than it was by leaf litter species (EBC vs. native). Finally, all shredder taxa, including limnephilid caddisflies, nemourid stoneflies and tipulid craneflies, grew on EBC leaf litter and sometimes were more than on the leaf litter of native species. Although limnephilid caddisflies feeding on EBC leaf litter actually decreased in size in 2009, this could be due to a decrease in food availability at the last removal date or the colonization by smaller instars of shredders rather than an indication of nutritional quality. Collectively, these data indicate that aquatic invertebrate shredders utilized EBC leaf litter as a food source in these streams.

While our results conflict with our hypothesis that shredders would be less likely to utilize EBC leaf litter inputs than native species, they are supported by previous studies. Grubbs and Cummins (1994) found that shredders in midwestern streams were abundant in *Prunus serotina* leaf packs. Another study found shredders colonized *Prunus padus* leaf litter at equal levels to alder and birch leaf litter in Scottish streams (Collen, 1994). One limiting factor to these studies is they consider shredder utilization of *Prunus* leaf litter in native habitats (Thompson & Townsend, 2003). However, our results are also supported by an experiment conducted in Anchorage streams finding no significant differences in survival or growth of *Psychoglypha* caddisflies when fed EBC leaf litter compared to mixed native/EBC leaf litter and exclusively native (alder and birch) leaf litter (Merrigan, 2011). These data complement our findings suggesting that shredders can survive and grow on EBC leaf litter at similar levels to the leaf litter of native species. It is still unknown whether, if given a choice, shredders would feed preferentially on EBC leaf litter. This question could be addressed via feeding bioassays.

Many studies have cited concerns that differences in leaf chemistry of invasive plant species can negatively affect leaf litter processing by shredders (Abelho & Graça, 1996; Sampaio *et al*., 2001; Braatne *et al*., 2007; Lecerf *et al*., 2007; Going & Dudley, 2008). While we did not analyze leaf chemistry in our study, we can still make conclusions about the suitability of EBC as a food source by looking at the functional response of shredders. In contrast to these studies, our data showed shredders fed on EBC leaf litter at similar levels to native species suggesting that any potential difference in leaf chemistry did not appear to have any significant effect on shredder communities. The rapid breakdown rate of EBC resulted in leaf litter that conditioned quickly in streams and provided a readily available food source for stream shredders. Our results align with the observations from Cummins *et al*. (1989) that shredders were less concerned with individual species of leaf litter than the state of leaf litter conditioning (Graça, 2001; Sampaio *et al*., 2001; Braatne *et al*., 2007; Lacan *et al*., 2010).

Although we detected no substantial ecological effects of EBC in these streams, the spread of EBC in riparian forests could have other ecological consequences we did not evaluate. The shift from native trees to EBC in riparian forests may alter the timing of leaf litter inputs entering streams. We observed EBC held onto its leaves later than other deciduous trees, delaying when leaf litter inputs enter the stream channel (Roon, *personal observation*). In addition to the delayed timing of inputs, the rapid breakdown of EBC leaf litter entering the stream at a single time could result in a pulse of resources that disappears quickly. Moline & Poff (2008) highlighted leaf litter retention as a concern with tamarisk in Colorado streams. If the phenology of leaf litter inputs does not match shredder life histories, a 'trophic mismatch' could result that reduces shredder abundance and affect litter processing in streams lined by riparian EBC (Strayer, 2010).

As EBC continues to spread in Alaska's riparian forests, it may also homogenize the diversity of leaf litter inputs available to shredders. Especially in streams lined by mixed deciduous forests, such as those of coastal Alaska, shredders receive a wide range of leaf litter inputs that enter the stream channel at different times and break down at different rates, providing shredders with what Peterson & Cummins (1974) referred to as a 'processing continuum' of resources. This 'processing continuum' of leaf litter inputs for shredders can be altered by the homogenization of these inputs (Peterson & Cummins, 1974). A study by Jonsson *et al*. (2001) found that shredder diversity in boreal streams was important for leaf litter processing. This supports the hypothesis made by Dangles *et al*. (2003) that invasive plants (in this case Japanese knotweed) can reduce the diversity of shredders and the shredders ability to process leaf litter in streams. Because shredders support other functional feeding groups of aquatic invertebrates, which collectively act as major prey sources for upper trophic level consumers, including stream fishes, the loss in shredder diversity could have detrimental effects on the functional integrity of streams (Cummins *et al*., 1989; Gessner & Chauvet, 2002; Baxter *et al*., 2005).

The shift in riparian vegetation from alder to EBC could have dramatic effects on stream food webs. Alder is an important source of nitrogen for stream and riparian ecosystems (Helfield & Naiman, 2002). Much research in Alaska has documented the value of alder for stream productivity, nutrient cycling and as a preferred food source for shredders and other aquatic invertebrates (Irons *et al*., 1988; Piccolo & Wipfli, 2002; Orlikowska *et al*., 2004). Thus, the loss of alder and spread of EBC in riparian forests could have perpetuating direct and indirect ecological effects in streams by decreasing the amount of nitrogen available for nutrient cycling or by changing the composition of leaf litter inputs in entering Alaskan streams (Lecerf *et al*., 2005; Strayer, 2010)

As invasive species continue to spread across landscapes, it is important to understand the ecological interactions and effects in their new environs (Strayer, 2010). This is especially true in riparian forests where the spread of invasive plants has the potential to affect both terrestrial and aquatic organisms, as well as the exchange of resources between the two (Baxter *et al*., 2005). It is difficult to predict which invasive species will be problematic, as previous studies have found varying and even conflicting results sometimes within the same species (Abelho & Graça, 1996; Lacan *et al*., 2010). Our study found that the spread of EBC in riparian forests does not appear to be markedly disrupting the ecological processes of leaf litter breakdown and aquatic invertebrate shredder colonization in these urban Alaska study streams. These results suggest that with respect to leaf litter processing by shredders, EBC appears to be functionally similar to native species. Collectively, these results provide clues about the extent to which invasive riparian plants can affect native species and ecological processes in stream ecosystems of Alaska.

Acknowledgements

We thank Dustin Merrigan, John Hill, Steve Ewest, Uinniq Ahgeak and Thomas Robertson for assistance with field and laboratory work. Thanks to Dan Rinella and Dan Bogan at ENRI for advice on the project design and providing summer lab space, and to

Arny Blanchard for his assistance with the statistical analysis. Thanks to the US Fish and Wildlife Service, USDA Forest Service, Institute of Arctic Biology and Alaska EPSCoR for funding this project.

References

Abelho, M. & Graça M.A.S. (1996) Effects of eucalyptus afforestation on leaf litter dynamics and macroinvertebrate community structure of streams in Central Portugal. *Hydrobiologia*, **324**, 195–204.

Alaska Natural Heritage Program (2006) Non-native species of Alaska: European Bird Cherry (*Prunus padus* L.). http://akweeds.uaa.alaska.edu.

Bailey, J.K., Schweitzer, J.A. & Whitham, T.G. (2001) Salt cedar negatively affects biodiversity of aquatic macroinvertebrates. *Wetlands*, **21**, 442-447.

Baxter, C.V., Fausch, K.D. & Saunders, W.C. (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology*, **50**, 201-220.

Benfield, E.F. (1996) Leaf breakdown in stream ecosystems. In: Methods in Stream Ecology (Eds F.R. Hauer & G.A. Lamberti), p 579–589. Academic Press, New York, NY.

Benke, A.C., Huryn, A.D., Smock, L.A. & Wallace, J.B. (1999) Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, **18**, 308-343.

Blossey, B. (1999) Before, during and after: the need for long-term monitoring in invasive plant species management. *Biological Invasions*, **1**, 301-311.

Braatne, J.H., Sullivan, S.M.P. & Chamberlain, E. (2007) Leaf decomposition and stream macroinvertebrate colonisation of Japanese knotweed, an invasive plant species. *International Review of Hydrobiology*, **92**, 656-665.

Carlson, M.L., Lapina, I.V., Shephard, M., Conn, J.S., Densmore. R., Spencer, P., Heys, J., Riley, J., & Nielsen, J. (2008) Invasiveness ranking system for non-native plants of Alaska. USDA Forest Service, R10, R10-TP-143, p 218.

Collen, P. (1994) The influence of riparian tree selection on stream invertebrate production. *Journal of Scottish Forestry*, **48**, 262-270.

Cummins, K.W., Wilzbach, M.A., Gates, D.M., Perry, J.B. & Taliaferro, W.B. (1989) Shredders and riparian vegetation: leaf litter that falls into streams influences communities of stream invertebrates. *BioScience*, **39**, 24-30.

Dangles, O., Jonsson, M. & Malmqvist, B. (2003) The importance of detritivore species diversity for maintaining stream ecosystem functioning following the invasion of a riparian plant. *Biological Invasions*, **4**, 441-446.

Dukes, J.S. & Mooney, H.A. (2004) Disruption of ecosystem processes in western North America by invasive species. *Natural History Review of Chil*e, **77**, 411-437.

Flagstad, L.A., Cortés-Burns, H. & Roberts, T.L. (2010) Invasive plant inventory and bird cherry control trials phase II: bird cherry distribution, demography, and reproduction biology along Chester and Campbell Creek trails, Anchorage, Alaska. *Alaska Natural Heritage Program*, p 61.

Friedman, J.M., Auble, G.T., Shafroth, P.B., Scott, M.L., Merigliano, M.F., Freehling, M.D. & Griffin, E.R. (2005) Dominance of non-native riparian trees in western USA. *Biological Invasions*, **7**, 747–751.

Gessner, M.O. & Chauvet, E. (2002) A case for using litter breakdown to assess functional stream integrity. *Ecology*, **12**, 498-510.

Going, B.M. & Dudley, T.L. (2008) Invasive riparian plant litter alters aquatic insect growth. *Biological Invasions*, **10**, 1041-1051.

Graça, M.A.S. (2001) The role of invertebrates on leaf litter decomposition in streams – a review. *International Review of Hydrobiology*, **86**, 383-393.

Gregory, S.V., Swanson, F.J., McKee, W.A. & Cummins, K.W. (1991) An ecosystem perspective of riparian zones. *BioScience*, **41**, 540-551.

Grubbs, S.A. & Cummins, K.W. (1994) Processing and macroinvertebrate colonization of black cherry (*Prunus serotina*) leaves in two streams differing in summer biota, thermal regime and riparian vegetation. *American Midland Naturalist*, **132**, 284-293.

Helfield, J. M. & Naiman, J.M. (2002) Salmon and alder as nitrogen sources to riparian forests in a boreal Alaskan watershed. *Oecologia*, **133**, 573-582.

Hood, W.G. & Naiman, R.J. (2000) Vulnerability of riparian zones to invasion by exotic vascular plants. *Plant Ecology*, **148**, 105-114.

Irons III, J.G., Oswood, M.W. & Bryant, J.P. (1988) Consumption of leaf detritus by a stream shredder: Influence of tree species and nutrient status. *Hydrobiologia*, **160**, 53-61.

Jonsson, M., Malmqvist, B. & Hoffsten, P.O. (2001) Leaf litter breakdown rates in boreal streams: does shredder species richness matter? *Freshwater Biology*, **46**, 161-171.

Kennedy, T.A. & Hobbie, S.E. (2004) Saltcedar (*Tamarix ramosissima*) invasion alters organic matter dynamics in a desert stream. *Freshwater Biology*, **49**, 65-76.

Lacan, I., Resh, V.H. & McBride, J.R. (2010) Similar breakdown rates and benthic macroinvertebrate assemblages on native and *Eucalyptus globulus* leaf litter in Californian streams. *Freshwater Biology*, **55**, 739-752.

Leather, S.R. (1996) *Prunus padus* L. *The Journal of Ecology*, **84**, 125-132.

Lecerf, A., Dobson, M., Dang, C.K. & Chauvet, E. (2005) Riparian plant species loss alters trophic dynamics in detritus-based stream ecosystems. *Oecologia*, **146**, 432-442.

Lecerf, A., Patfield, D., Boiché, A., Riipinen, M.P., Chauvet, E. & Dobson, M. (2007) Stream ecosystems respond to riparian invasion by Japanese knotweed (*Fallopia japonica*). *Canadian Journal of Fisheries and Aquatic Sciences*, **64**, 1273-1283.

Mack, R.M., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689-710.

Merrigan, D. (2011) Growth and mortality of caddisfly (*Psychoglypha* spp.) larvae reared on native and invasive European bird cherry leaf litter. Thesis, Alaska Pacific University.

Merritt R.W. & Cummins K.W. (1996) An introduction to the aquatic insects of North America. Kendall⁄Hunt Publishing Company, Dubuque, IA.

Milner, A.M. & Oswood, M.W. (2000) Urbanization gradients in streams of Anchorage, Alaska: a comparison of multivariate and multimetric approaches to classification. *Hydrobiologia*, **422**, 209-223.

Moline, A.B. & Poff, N.L. (2008) Growth of an invertebrate shredder on native (*Populus*) and non-native (*Tamarix*, *Elaeagnus*) leaf litter. *Freshwater Biology*, **53**, 1012-1020.

Motomori, K., Mitsuhashi, H. & Nakano, S. (2001) Influence of leaf litter quality on the colonization and consumption of stream invertebrate shredders. *Ecological Research*, **16**, 173-182.

Orlikowska, E.H., Deal, R.L., Hennon, P.E. & Wipfli, M.S. (2004) The role of red alder in riparian forest structure along headwater streams in southeastern Alaska. *Northwest Science*, **78**, 111-123.

Ourso, R.T. & Frenzel, S.A. (2003) Identification of linear and threshold responses in streams along a gradient of urbanization in Anchorage, Alaska. *Hydrobiologia*, **501**, 117-131.

Petersen, R.C. & Cummins, K.W. (1974) Leaf processing in a woodland stream. *Freshwater Biology*, **4**, 343-368.

Piccolo, J.J. & Wipfli, M.S. (2002) Does red alder (*Alnus rubra*) in upland riparian forests elevate macroinvertebrate and detritus export from headwater streams to downstream habitats in southeastern Alaska? *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 503-513.

Planty-Tabacchi, A.M., Tabacchi, E., Naiman, R.J., Deferrari, C. & Décamps, H. (1996) Invasibility of species-rich communities in riparian zones. *Conservation Biology*, **10**, 598–607.

Royer, T.V., Monaghan, M.T. & Minshall, G.W. (1999) Processing of native and exotic leaf litter in two Idaho (USA) streams. *Hydrobiologia*, **400**, 123–128.

Ruess, R.W., McFarland, J.M., Trummer, L.M. & Rohrs-Richey, J.K. (2009) Disease-mediated declines in N-fixation inputs by *Alnus tenuifolia* to early-successional floodplains in interior and south-central Alaska. *Ecosystems*, **12**, 489-502.

Sampaio, A., Cortes, R. & Leão, C. (2001) Invertebrate and microbial colonisation in native and exotic leaf litter species in a mountain stream. *International Review of Hydrobiology*, **86**, 527-540.

Sher, A.A., Marshall, D.L. & Taylor, J.P. (2002) Establishment patterns of native *Populus* and *Salix* in the presence of invasive nonnative *Tamarix*. *Ecological Applications*, **12**, 760–772.

Strayer, D. (2010) Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology*, **55**, 152-174.

Thompson, R.M. & Townsend, C.R. (2003) Impacts on stream food webs of native and exotic forest: an intercontinental comparison. *Ecology*, **84**, 145-161.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130-137.

Wallace, J.B., Eggert, S.L., Meyer, J.L. & Webster, J.R. (1997) Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science*, **277**, 102-104.

Webster, J.R. & Benfield, E.F. (1986) Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics*, **17**, 567–594.

Table 2.1. Study site characteristics of leaf pack experiments in Campbell and Chester creeks.

Parameter	Stream and Site Chester Creek (*urbanized*)	(*reference*)	Campbell Creek (*urbanized*)	(*reference*)
GPS Location	N: 61.19284 W: -149.83014	N: 61.20366 W: -149.79013	N: 61.14754 W: -149.89041	N: 61.16865 W: -149.7634
Elevation (m)	60	71	12	98
Canopy Cover (%)	92.5	89.6	37.8	74.0
Canopy Composition	B>EBC>A>S	S>A>B>EBC	A>B>EBC>S	A>B>C>S
Stream Width (m)	3.6	2.8	11.5	5.7
Discharge ($m^3 \cdot s^{-1}$)	0.55	0.11	2.43	0.72
Stream Temp (˚C)	12.4	6.2	10.1	8.7
pH	7.9	7.5	8.0	7.6
Conductivity ($\mu S \cdot cm^{-1}$)	236	273	116	148

Canopy composition species include A= Alder, B= Birch, C= Cottonwood, EBC= European bird cherry, S= Spruce.

Table 2.2. Breakdown rates (*k*) of EBC and native leaf litter. Breakdown rates (*k*) were calculated per day and per degree day for both leaf pack experiments in Chester and Campbell creeks.

Stream Site	Degree Days	Leaf Species	*k* (day)	r^2	*P*-value vs. EBC*	*k* (degree day)	r^2	*P*-value vs. EBC*
<u>2009</u>								
Chester	854	Alder	0.0691	0.92	**0.046**	0.0052	0.92	**0.044**
-*urbanized*		Birch	0.0650	0.87	**0.005**	0.0048	0.87	**0.005**
		Cottonwood	0.0495	0.82	**<0.001**	0.0037	0.83	**<0.001**
		EBC	0.0821	0.86		0.0061	0.86	
<u>2010</u>								
Chester	672	Alder	0.0569	0.90	**0.015**	0.0044	0.91	**0.014**
-*urbanized*		EBC	0.0772	0.88		0.0060	0.89	
Chester	333	Alder	0.0267	0.93	**0.008**	0.0042	0.93	**0.009**
-*reference*		EBC	0.0512	0.94		0.0081	0.94	
Campbell	545	Alder	0.0287	0.97	0.089	0.0027	0.96	0.106
-*urbanized*		EBC	0.0377	0.90		0.0036	0.89	
Campbell	470	Alder	0.0395	0.86	0.102	0.0044	0.85	0.114
-*reference*		EBC	0.0665	0.87		0.0073	0.85	

* Numbers in bold indicate that the differences between native species and EBC are statistically significant ($P < 0.05$).

Table 2.3. Shredder composition associated with EBC and native leaf litter. The percent composition of shredder taxa by count and biomass (mg) present in leaf packs for leaf pack experiments in 2009 and 2010.

		Shredder Taxa					
Stream	Leaf	Limnephilidae		Nemouridae		Tipulidae	
Site	Species	Count	Mass	Count	Mass	Count	Mass
2009							
Chester	Alder	66.1	98.0	32.2	1.0	1.7	1.0
-urbanized	Birch	69.4	91.9	29.1	1.5	1.5	6.6
	Cottonwood	36.7	95.9	63.3	4.1	0.0	0.0
	EBC	77.0	99.1	23.0	0.9	0.0	0.0
2010							
Chester	Alder	76.2	97.1	23.2	2.8	0.6	0.1
-urbanized	EBC	73.0	95.4	22.5	2.6	4.5	2.0
Chester	Alder	94.9	98.1	1.3	0.1	3.8	1.8
-reference	EBC	98.6	99.8	0.0	0.0	1.4	0.2
Campbell	Alder	72.0	94.8	24.6	2.7	3.4	2.5
-urbanized	EBC	67.0	88.5	16.9	2.4	16.1	9.1
Campbell	Alder	12.3	63.1	85.6	35.4	2.1	1.5
-reference	EBC	8.2	39.5	90.2	59.3	1.6	1.2

Table 2.4. Shredder growth associated with EBC and native leaf litter. Growth was calculated by the percent change in length (mm) over the duration of each leaf pack experiment for each shredder taxa for both 2009 and 2010 leaf pack experiments.

	Shredder Growth		
Leaf Species	Limnephilidae	Nemouridae	Tipulidae
2009			
Alder	-23.4	39.8	0.0
Birch	45.7	36.7	0.0
Cottonwood	85.0	37.8	-
EBC	-20.6	42.9	-
2010			
Alder	15.5	36.7	65.7
EBC	42.7	41.2	10.2

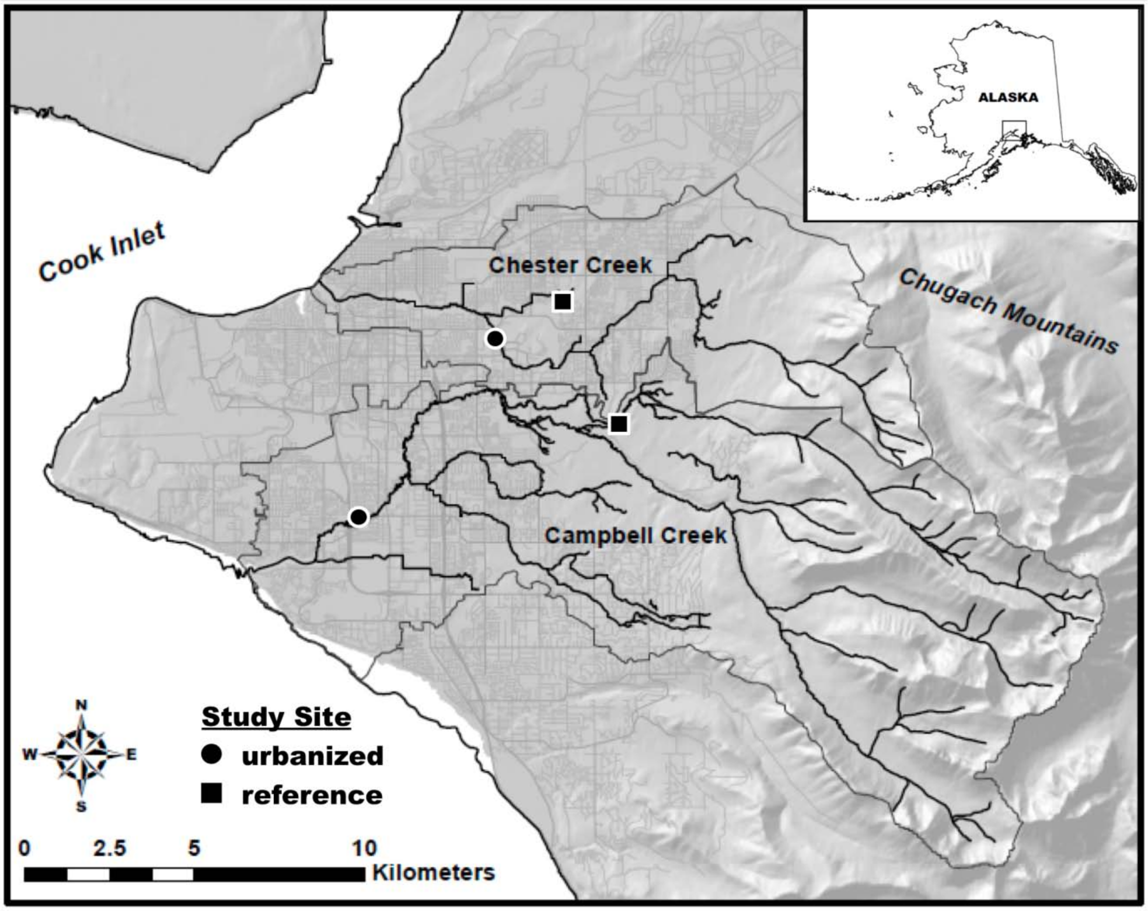

Fig. 2.1. Map of leaf pack study sites in Campbell and Chester creeks.

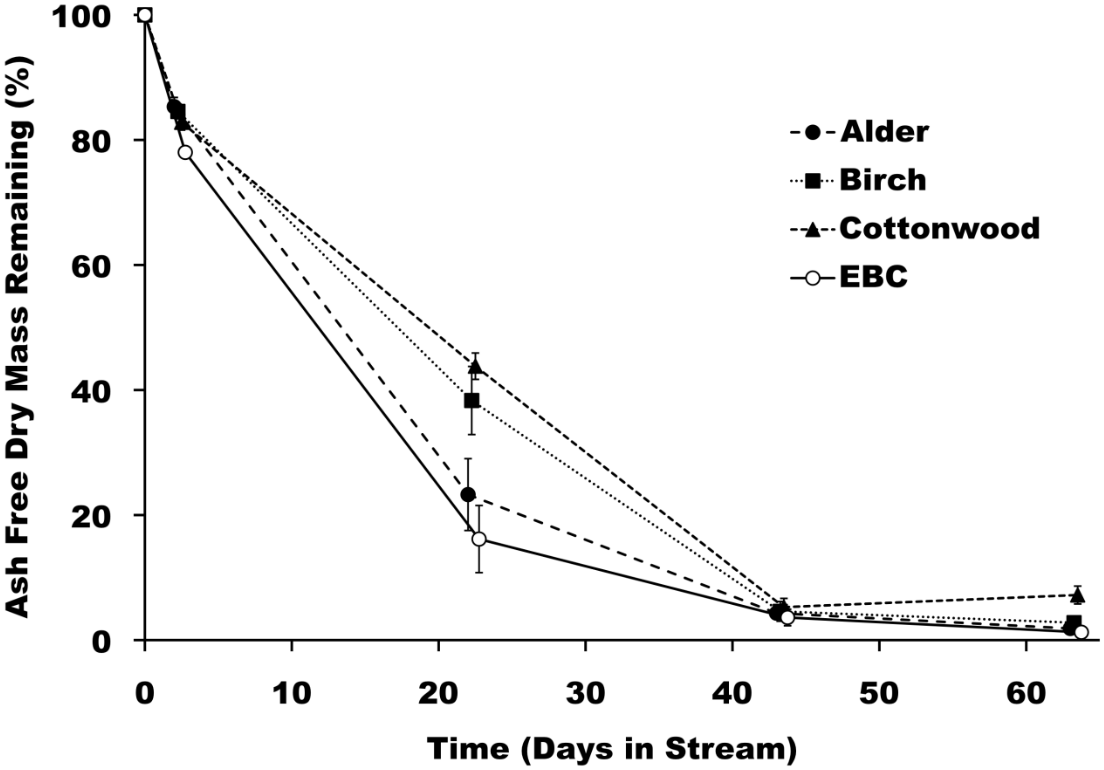

Fig. 2.2. Breakdown of EBC and native leaf litter in Chester Creek in 2009. Percent of ash free dry mass that was remaining over time for EBC and native alder birch and cottonwood leaf packs deployed in the Chester Creek urbanized site in 2009. Error bars represent standard errors.

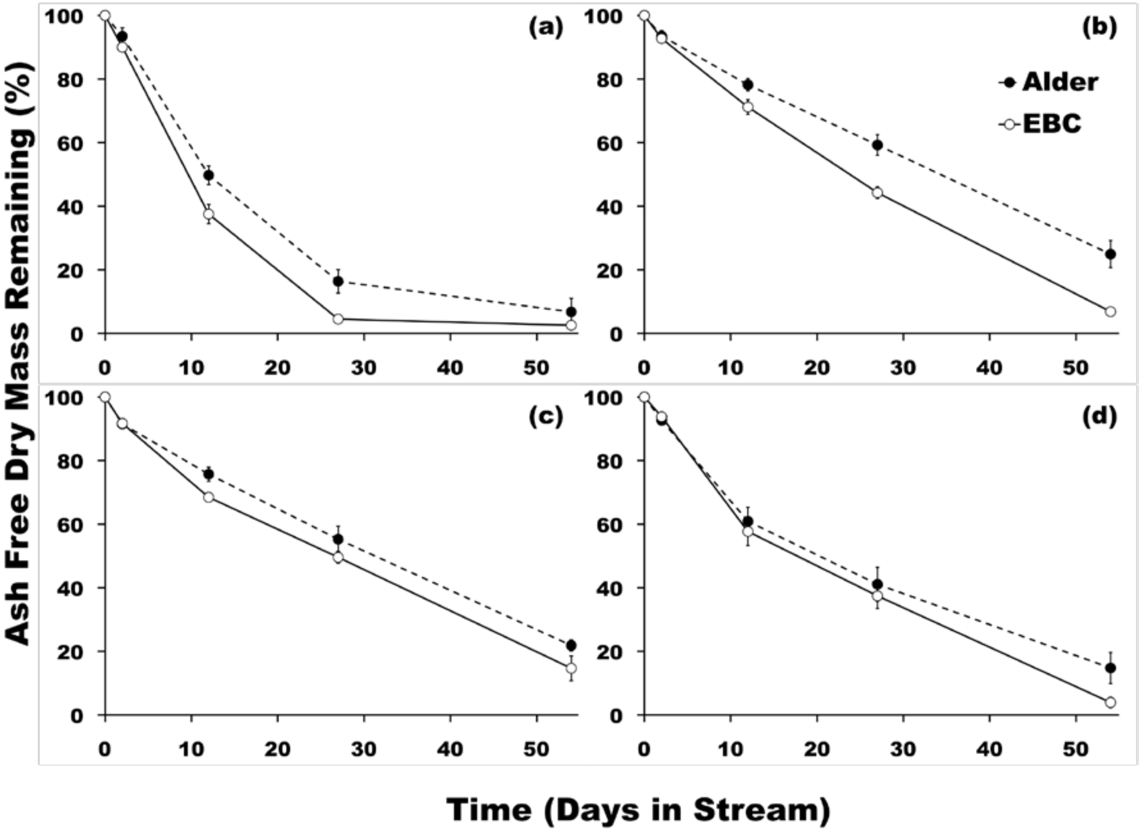

Fig. 2.3. (a-d) Breakdown of EBC and alder leaf litter in Campbell and Chester creeks in 2010. Percent of ash free dry mass that was remaining over time for EBC and native alder leaf packs deployed in a) Chester Creek urbanized site, b) Chester Creek reference site, c) Campbell Creek urbanized site, and d) Campbell Creek reference site in 2010. Error bars represent standard errors.

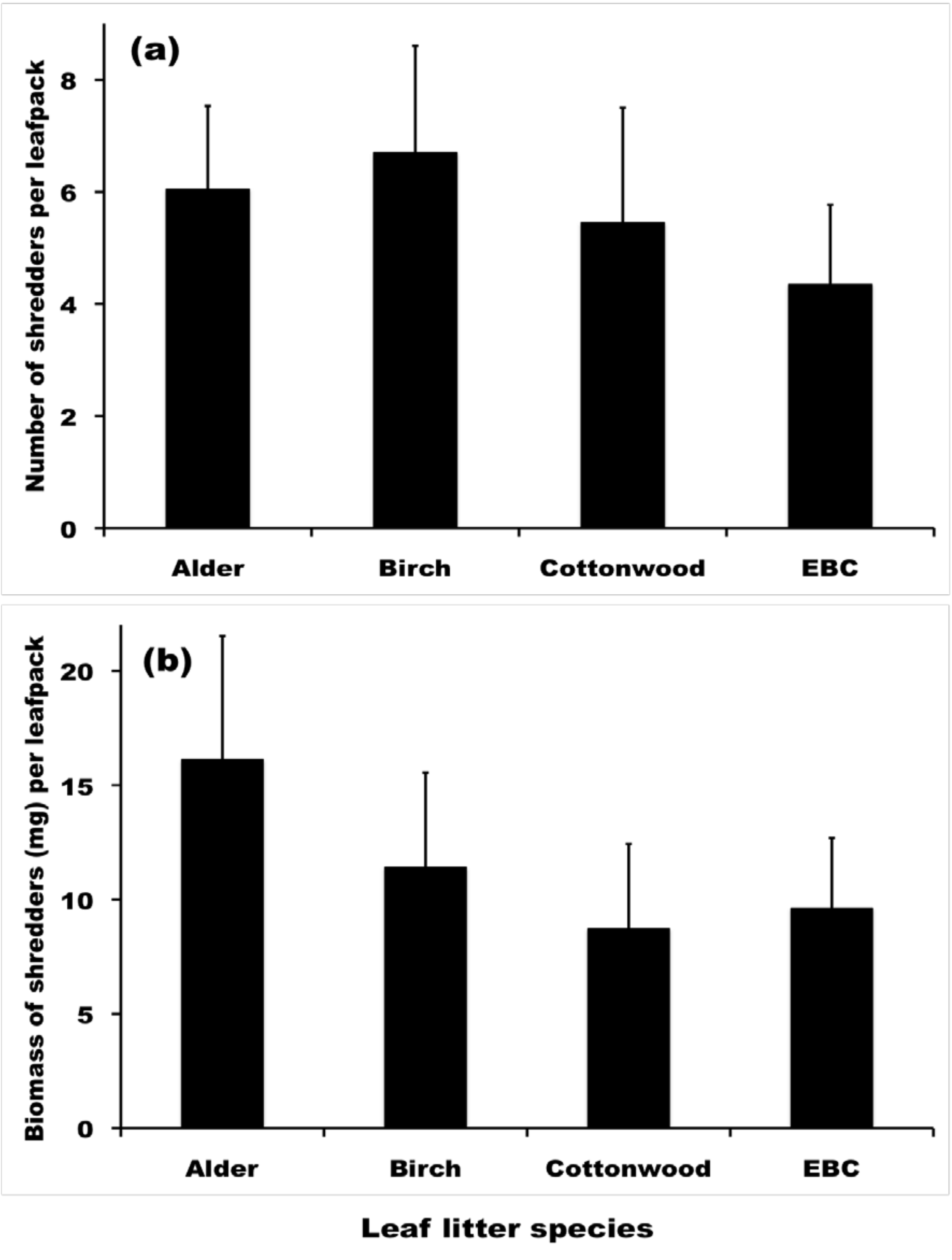

Fig. 2.4. (a-b) Abundance and biomass of aquatic invertebrate shredders in 2009. Mean abundance (a) and biomass (b) of shredders that were associated with EBC and native alder, birch and cottonwood leaf packs in the Chester Creek urbanized site in 2009. Error bars represent standard errors.

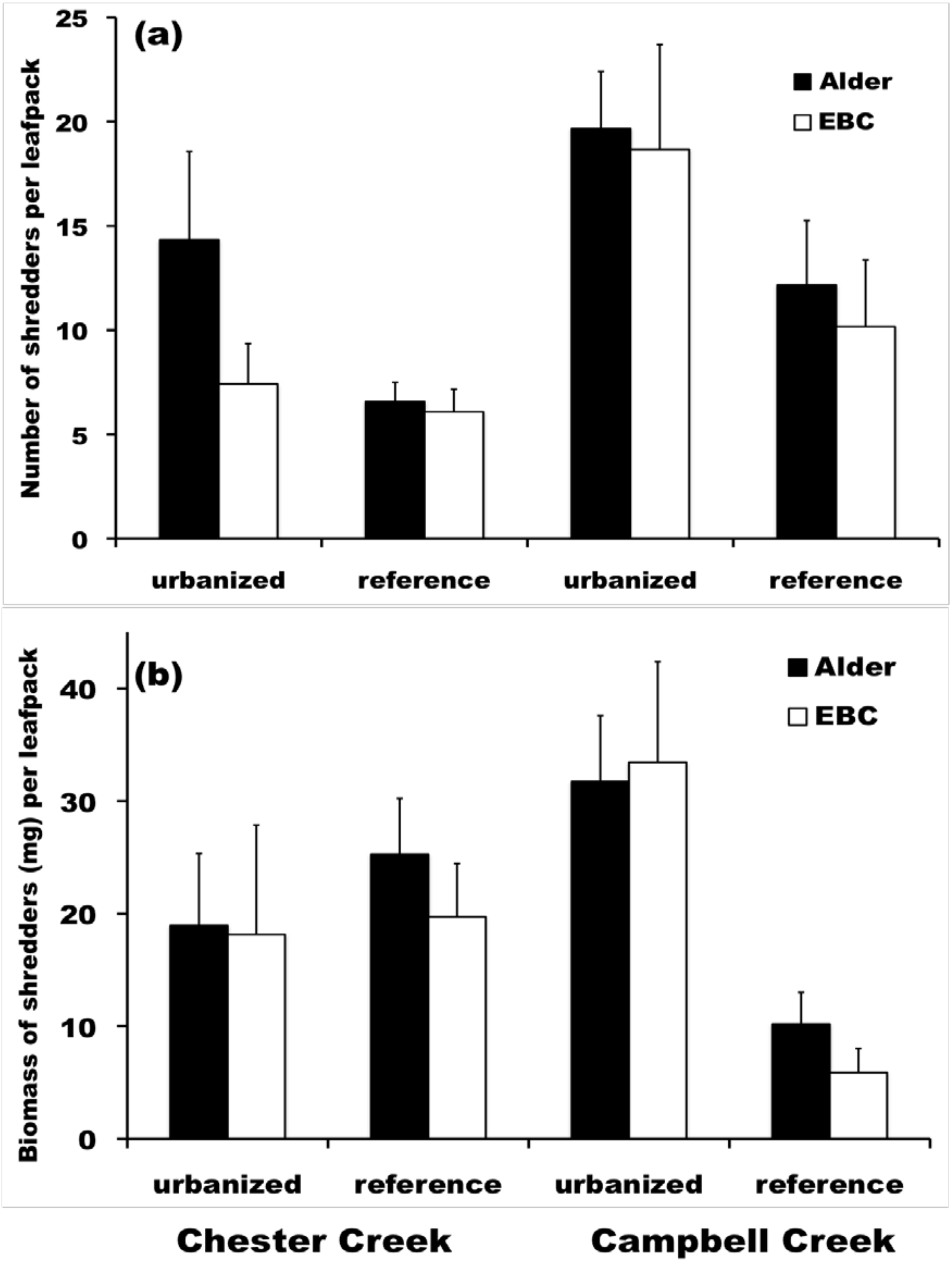

Fig. 2.5. (a-b) Abundance and biomass of aquatic invertebrate shredders in 2010. Mean abundance (a) and biomass (b) of shredders that were associated with EBC and native alder leaf packs in Campbell and Chester creek in reference and urbanized sites in 2010. Error bars represent standard errors.

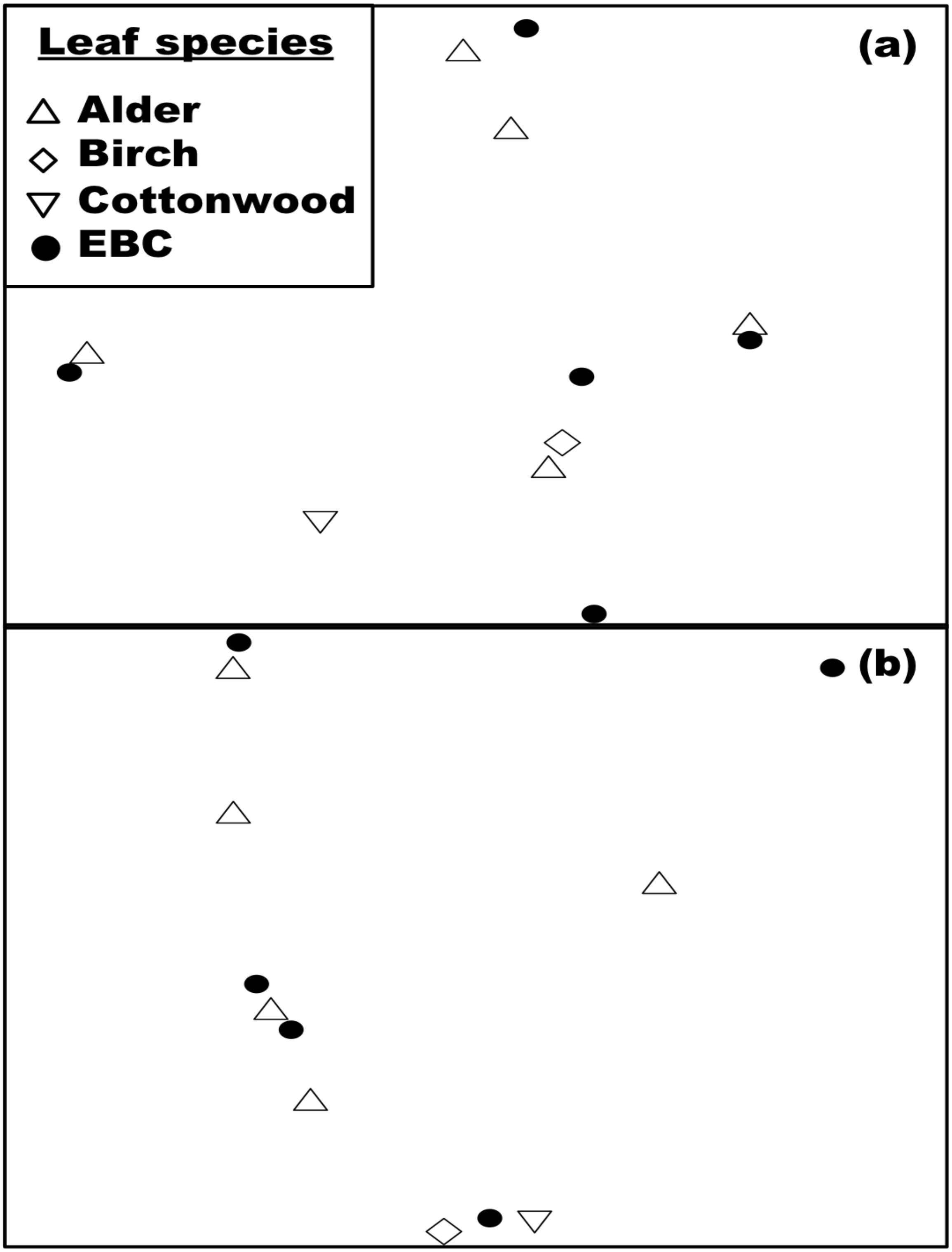

Fig. 2.6. (a-b) Community structure of aquatic invertebrate shredders. NMDS ordination plots comparing shredder community structure between EBC and native leaf species from both leaf pack experiments by (a) mean abundance and (b) mean biomass.

Chapter 3

Invasive European bird cherry disrupts stream-riparian linkages: influence on terrestrial invertebrate prey subsidies for juvenile coho salmon[1]

Abstract

European bird cherry (*Prunus padus*) (EBC) is an invasive tree that is rapidly spreading and possibly displacing native riparian trees along streams in parts of urban Alaska. The spread of EBC may affect stream-riparian linkages, including terrestrial prey subsidies to stream consumers. To examine whether riparian EBC is affecting terrestrial invertebrate prey abundance and subsidies for stream salmonids, we sampled terrestrial invertebrates on the foliage of riparian tree branches, their inputs into streams collected by floating pan traps, and consumption by juvenile coho salmon (*Oncorhynchus kisutch*) in two Anchorage, Alaska streams, Campbell and Chester creeks. Foliage on EBC branches supported a significantly lower biomass of terrestrial invertebrates than the native deciduous trees thin-leaf alder (*Alnus tenuifolia*) and paper birch (*Betula neoalaskana*), but a significantly greater biomass than spruce (*Picea* spp.). EBC contributed significantly lower inputs of terrestrial invertebrate biomass to streams than mixed native vegetation in both Campbell and Chester creeks. We did not detect significantly different amounts of ingested terrestrial invertebrates by fish between EBC and native tree patches along streams. Community structure and overlap of terrestrial invertebrates varied between years, not showing any clear negative effect of EBC on prey resources for fish. Although EBC is affecting the abundance and availability of terrestrial invertebrates, we did not detect a direct effect on prey resources consumed by juvenile coho salmon in these streams. Lowered prey abundance as measured in this study may have long-term consequences for stream salmonids as EBC continues to spread along streams over time.

---

[1] Roon, D.A., M.S. Wipfli, T.L. Wurtz and A.L. Blanchard. Invasive European bird cherry disrupts stream-riparian linkages: influence on terrestrial invertebrate prey subsidies for juvenile coho salmon. Prepared for submission to Canadian Journal for Fisheries and Aquatic Sciences.

Introduction

Invasive plant species are a concern worldwide because they can displace native species, reduce biodiversity and disrupt ecological processes (Wilcove et al. 1998; Dukes and Mooney 2004). Invasive plants can grow in dense patches, outcompeting nearby native species for resources (e.g. light, water and nutrients) (Friedman et al. 2005; Kennedy et al. 2005). They can also exhibit allelopathic properties, negatively affecting germination and growth of native species (Hierro and Callaway 2003). As a result, invasive plants are spreading in many locations across the world (Sher et al. 2002; Dukes and Mooney 2004; Friedman et al. 2005; Ringold et al. 2008)

Riparian zones are highly susceptible to the spread of invasive plants (Gregory et al. 1991; Hood and Naiman 2000). The combination of flood events that disturb riparian soils and extensive habitat connectivity create ideal conditions for invasive plants to spread (Hood and Naiman 2000). As a result, riparian forests often contain a higher number of invasive plants than upland habitats (Planty-Tabacchi et al. 1996; Hood and Naiman 2000). Because riparian zones link terrestrial and aquatic ecosystems, the spread of invasive plants in riparian forests can affect stream organisms and food webs (Gregory et al.1991; Hood and Naiman 2000; Baxter et al. 2005).

One pathway through which riparian zones link terrestrial and aquatic ecosystems is through the inputs of terrestrial invertebrates for aquatic consumers. Drift-feeding fishes like stream salmonids feed on aquatic invertebrates drifting through the water column, but also rely on terrestrial invertebrates as seasonal prey resources (Wipfli 1997; Nakano and Murakami 2001; Allan et al. 2003). Previous studies have documented the importance of terrestrial invertebrates as prey for stream salmonids in many locations including SE Alaska (Wipfli 1997; Allan et al. 2003), the Pacific Northwest (Romero et al. 2005), Japan (Nakano and Murakami 2001; Kawaguchi et al. 2003), the Kamchatka Peninsula, Russia (Eberle and Stanford 2010) and to a lesser extent in New Zealand (Edwards and Huryn 1995). Nakano et al. (1999b) determined that rainbow trout selectively fed on terrestrial invertebrates at elevated levels relative to their availability drifting in Japanese streams. Another Japanese study found that experimentally reducing inputs of terrestrial invertebrates affected salmonid abundance and distribution in streams (Kawaguchi et al. 2003).

The abundance of terrestrial invertebrate communities can vary widely between vegetation types (Mason and MacDonald 1982). The ‘resource quality hypothesis’ predicts that terrestrial invertebrate herbivores are more likely to feed on vegetation types that are higher in nutrient content and lack secondary compounds (Schowalter et al. 1986; Ober and Hays 2008). As a result, the spread of invasive plants in riparian forests can affect terrestrial invertebrate communities if their tissues differ in quality from native species (Mason and MacDonald 1982; Ober and Hays 2008). Observational field studies have documented declines in terrestrial invertebrate abundance and species richness relative to native vegetation with invasive willows in Australia (Greenwood et al. 2004), giant reed in California (Herrera and Dudley 2003), Japanese knotweed in Europe (Gerber et al. 2008) and tamarisk in the American southwest (Wiesenborn 2005). While the Greenwood et al. (2004) study documented that invasive willow reduced stream inputs of terrestrial invertebrates, little research has addressed the effects of invasive riparian plants on terrestrial invertebrate communities to stream food webs or to upper trophic level consumers like stream fishes. A study by Glova and Sagar (1994) in New Zealand found streams lined with invasive willow supported a higher abundance of invertebrate prey for brown trout than streams lined by native vegetation. In contrast, Kennedy et al. (2005) found that the eradication of invasive tamarisk increased fish densities in Colorado streams. Considering the limited scope and conflicting results of these two studies, this topic warrants further investigation.

European bird cherry (*Prunus padus*) (EBC) is an ornamental tree frequently planted in Alaska for its showy floral display, outside of its native range (Alaska Natural Heritage Program 2006). Birds feed on the cherries and transport the seeds from source trees to adjacent natural areas creating wild populations over time (Alaska Natural Heritage Program 2006). Able to tolerate a wide range of climates and habitat types in its native Europe, EBC thrives in cold climates and wet soils, making it well suited for riparian zones in Alaska (Leather 1996). EBC has spread rapidly in the last 10 years, and appears to be displacing native trees in riparian forests along streams in parts of urban Alaska (Flagstad et al. 2010). EBC is able to form dense, monotypic stands, and is ranked as ‘highly invasive’ (Carlson et al. 2008).

At the same time, the dominant riparian tree species, thin-leaf alder (*Alnus tenuifolia*), appears to be decreasing across southcentral Alaska due to the combined effects of a canker and invasive insect pests (Ruess et al. 2009). Known to be a nitrogen fixer, riparian alder is thought to act as an important source of nitrogen for riparian and stream ecosystems (Helfield and Naiman 2002). Alder-dominated forests in headwater streams also contributed elevated levels of invertebrates to streams compared to conifer forests. These inputs supported stream salmonids occupying habitats further downstream (Piccolo and Wipfli 2002; Wipfli and Gregovich 2002; Wipfli and Musslewhite 2004). Similarly a shift in riparian vegetation from alder to EBC could have dramatic effects on stream food webs. Given that terrestrial invertebrates are important prey resources for stream salmonids, the spread of EBC in riparian forests could negatively affect salmonid production in Alaskan streams.

The objective of this study was to examine if riparian EBC is affecting terrestrial invertebrate prey resources for juvenile coho salmon (*Oncorhynchus kisutch*) in Campbell and Chester creeks in Anchorage, Alaska. We hypothesized that EBC negatively affects 1) abundance of terrestrial invertebrates on riparian plants, 2) flow of terrestrial invertebrate prey subsidies to streams, and 3) ingestion of terrestrial invertebrates by stream salmonids. Demonstrating that EBC negatively affects energy flow to streams and predation rates by fishes will aid land management agencies in their invasive species control programs and with managing riparian forests in urban Alaska.

Methods

Study sites

This study focused on two Anchorage streams, Campbell and Chester creeks, with sampling taking place May-September, in 2009 and 2010. Chester Creek is a second-order stream with a watershed covering 78 km^2 and Campbell Creek is a fourth-order stream covering 202 km^2. Located in the southcentral part of the state (61°10’N, 149°45’W), Anchorage is characterized by a coastal climate considered to be a transitional zone between boreal and temperate rainforest biomes (Milner and Oswood 2000). Originating in the Chugach Mountains, these streams flow west through the urbanized lowlands of the Anchorage bowl before ultimately reaching the saltwater of Cook Inlet (Figure 3.1). Greenbelt corridors of municipal parkland parallel the lower portions of both streams, keeping the riparian zones largely intact as they flow through Alaska’s largest city (Ourso and Frenzel 2003). Native riparian vegetation is composed of mixed deciduous and coniferous forests dominated by spruce (*Picea* spp.), alder (*Alnus* spp.), paper birch (*Betula neoalaskana*), cottonwood (*Populus trichocarpa*), and willow. EBC is widespread along the lower, urbanized portions of these watersheds, completely displacing native riparian vegetation in places (Chapter 1). Both streams support wild populations of rearing and spawning Pacific salmon (*Oncorhynchus* spp.).

Sampling occurred in two sites delineated by riparian vegetation type: a ~150-m reach dominated by EBC and a second ~150-m reach approximately 200 m upstream dominated by native riparian trees, in and along both creeks.

Site characterization

We surveyed riparian canopy cover and composition overhanging the stream channel by measuring total canopy cover, % EBC and canopy composition with a handheld densiometer at 15-m intervals throughout each study site and averaged together. Stream width was measured at 15 m intervals throughout each study site and averaged together. Discharge was calculated using monthly flow measurements taken with a flow meter (Flo-Mate 2000, Marsh-McBirney Inc., Hach, CO). Stream temperature, pH and conductivity were measured monthly with a Hanna combination meter® to characterize in-stream conditions (Hanna Instruments, Woonsocket, RI).

Terrestrial invertebrates associated with riparian trees

To compare terrestrial invertebrate communities associated with EBC relative to native riparian trees, we sampled terrestrial invertebrates present on the foliage of riparian tree branches, following the methods outlined by Allan et al. (2003). To do this, we clipped a branch of a single tree species growing within 1 m of the stream channel and 1 m above the ground into a plastic garbage bag containing insecticide (pyrethrin strip), being careful not to disturb insects present. This was repeated for EBC and three native species common in the riparian zones of these streams: thin-leaf alder, paper birch and spruce. Three replicate samples were collected from each species in two locations from each stream over four monthly intervals during the summer for a total sample size of 204 in 2009 and 192 in 2010. All invertebrates found on branches were stored in vials filled with 70% ethanol and later identified to family, enumerated and their length measured to estimate biomass using published length weight regressions (Sample et al.1993, Sabo et al. 2002). While adult life stages of aquatically derived taxa were also found, we focused exclusively on taxa that we could confidently identify as terrestrially derived. This excluded many individuals in the order Diptera. All foliage was removed from the stem and dried at 60 ˚C for 24 hours to measure leaf dry mass. Total invertebrate biomass was divided per gram of leaf mass to standardize terrestrial invertebrate mass between samples.

Stream inputs of terrestrial invertebrates

We used floating pan traps to compare stream inputs of terrestrial invertebrates between reaches lined by EBC and native vegetation. We set out pan traps constructed of plastic dishpans (~1000 cm^2 surface area) supported by a foam square that floated on the stream surface and was tethered to the streambank, following the methods described by

Wipfli (1997) and Allan et al. (2003). Dishpans were filled with ~ 5L stream water and small amount of dish soap to break the water tension, ensuring that insects would not escape. Four to five replicate pan traps were placed underneath patches of EBC or of mixed native vegetation for three days in both Campbell and Chester creeks. Contents for each pan were sieved through at 250 um mesh and were stored in Whirl-paks® (Nasco, Fort Atkinson, WI) and filled with 90% ethanol to be processed later in the lab. This was repeated monthly throughout the summer for a total sample size of 68 in 2010. In the lab, invertebrates were identified to family, enumerated and length measured to estimate biomass using published length weight regressions (Sample et al. 1993, Sabo et al. 2002). While we found adult life stages of aquatically derived taxa, we focused on taxa we could identify as terrestrially derived.

Juvenile coho salmon ingestion of terrestrial invertebrates

We collected diet samples from juvenile coho salmon to determine whether riparian EBC affected prey intake of terrestrial invertebrates by stream salmonids relative to fish in streams lined by native riparian trees. Juvenile coho salmon (fork length 60 – 120 mm) were captured with minnow traps placed in pool habitats and baited with salmon roe following the methods outlined by Wipfli (1997) and Allan et al. (2003). At each site, fish were anaesthetized with MS-222® (Argent Chemical Laboratories Inc., Redmond, WA), mass and fork length measured, and then the stomach contents flushed from the fish with a soft-tipped 10 ml plastic syringe filled with water. Stomach contents were stored in Whirl-paks® and filled with 95% ethanol. All fish were returned to the same location where they were originally caught after the anesthetic wore off completely. Fifteen fish were caught in each site (one lined by EBC and one lined by native riparian trees) in both Campbell Creek and Chester Creek. This sampling was repeated monthly for a total sample size of 240 fish in 2009 and 189 fish in 2010. To help ensure invertebrates in coho diets were a reflection of the invertebrates simultaneously occurring in the environment, we sampled fish diet within 1 to 2 days and in the same sites as the branch and pan trap sampling. Samples were later processed in the lab, where invertebrates were identified to family, enumerated and measured to estimate biomass using published length weight regressions (Sample et al. 1993, Sabo et al. 2002). As mentioned before, we focused exclusively on taxa that we could identify as terrestrially derived.

Statistical analysis

We compared the biomass of terrestrial invertebrates between EBC and native riparian trees using a repeated measures ANOVA where vegetation type (EBC vs. native) and date were used as predictor variables. To account for differences between streams, we used a nested design, where sites (EBC vs. native) were nested within streams and samples were nested within site. This model was used to compare the biomass of terrestrial invertebrates associated with riparian tree branches, their inputs into streams and consumption by juvenile coho salmon. Because biomass data did not initially meet assumptions of normality or equal variance, we applied a log (x + 1) transformation. While figures show pre-transformed data, all statistical analysis used transformed data. ANOVAs were run using PROC-MIXED in SAS (SAS Institute Inc., version 9.2).

To test whether EBC affected the composition of terrestrial invertebrate communities, we compared the terrestrial invertebrate community structure present on riparian branches, their inputs into streams, and consumption by juvenile coho salmon. We ran a cluster analysis and a nonmetric multidimensional scaling (NMDS) ordination on a Bray-Curtis similarity matrix using percent composition by biomass to look for groupings among these categories. We overlayed circles on the NMDS ordination plots to reflect natural groupings present in cluster analysis. We quantified overlap with a percent similarity index (PSI %) using the model $PSI = 1 – 0.5 \bullet \sum |p_i - q_i|$ where p_i and q_i are the proportion of prey category *i* in groups *p* and *q* to compare if terrestrial invertebrates associated with different vegetation types (EBC vs. native) influenced coho diet differently. The PSI values range from 0 (no overlap) to 1 (complete overlap) (Hurlbert 1978). Community analyses were run in R (R Development Core Team, version 2.10.1).

Results

Site characteristics

Study sites were lined by a mix of EBC and native trees, primarily spruce, alder and birch. Riparian canopy cover over the stream channel ranged between 21 and 54% of study reaches, with higher canopy cover in EBC sites than native sites (Table 3.1). Chester Creek sites were narrower in stream width, lower in stream discharge, and slightly higher in stream temperature and conductivity than Campbell Creek sites (Table 3.1). Juvenile coho salmon caught in Chester Creek were slightly larger by fork length and mass than in Campbell Creek (Table 3.1).

Terrestrial invertebrates associated with riparian trees

Terrestrial invertebrates were abundant on all species of riparian trees sampled throughout the summer. Thirteen orders of terrestrial invertebrates were identified on riparian tree branch samples. Wasps (Hymenoptera), true bugs (Homoptera), spiders (Arachnida) and moths (Lepidoptera) were the most common taxa by biomass (Tables 3.2 & 3.3). Taxa in the sawfly family Tenthredinidae (Hymenoptera) were the most abundant family for native deciduous trees (Tables 3.2 & 3.3). Sawflies were abundant on alder branches, accounting for 53% of the biomass in 2009 and 63 % in 2010. Sawflies were also abundant on birch branches, accounting for 13% in 2009 and 33% of the biomass in 2010. EBC branches supported mostly spiders, true bugs including aphids and hoppers, and adult wasps (Tables 3.2 & 3.3). Spruce branches supported mostly spiders and adult wasps (Tables 3.2 & 3.3).

Terrestrial invertebrate biomass varied by tree species and by date in 2009 and 2010. In 2009, while terrestrial invertebrate biomass did not vary between streams ($F_{1,137} = 0.23$, $P = 0.630$) or by sites nested within stream ($F_{1,137} = 1.04$, $P = 0.309$), there was a significant effect of vegetation type nested within site ($F_{6,137} = 27.23$, $P < 0.001$), an effect of date ($F_{7,137} = 3.27$, $P = 0.003$) and a vegetation type x date interaction ($F_{51,137} = 2.74$, $P < 0.001$). Patterns were similar in 2010, where terrestrial invertebrate biomass did not vary between streams ($F_{1,128} = 1.39$, $P = 0.240$), date ($F_{6,128} = 1.08$, $P = 0.376$), or site nested within stream ($F_{1,128} = 3.33$, $P = 0.071$), but there was a significant effect of vegetation type nested within site ($F_{6,128} = 21.96$, $P < 0.001$) and a vegetation type x date interaction ($F_{48,128} = 2.15$, $P < 0.001$). Native deciduous trees, alder and birch, supported significantly more biomass than EBC in 2009 and 2010 ($P < 0.001$ for both species in both years) while EBC supported a significantly higher biomass than spruce in 2009 and 2010 ($P < 0.001$ for both years). Alder supported the highest mean biomass of all species sampled, supporting an average terrestrial invertebrate biomass of 3.6 $\text{mg}\cdot\text{g}^{-1}$ leaf mass in 2009 and 3.4 $\text{mg}\cdot\text{g}^{-1}$ leaf mass in 2010 (Figure 3.2). Birch supported the second highest mean biomass of terrestrial invertebrates with an average of 3.1 $\text{mg}\cdot\text{g}^{-1}$ leaf mass in 2009 and 2.9 $\text{mg}\cdot\text{g}^{-1}$ leaf mass (Figure 3.2). EBC supported less biomass compared to the native deciduous trees, with 0.5 $\text{mg}\cdot\text{g}^{-1}$ leaf mass in 2009 and 0.8 $\text{mg}\cdot\text{g}^{-1}$ leaf mass in 2010 (Figure 3.2). Spruce, the only conifer we sampled, supported the lowest biomass of terrestrial invertebrates with an average biomass of 0.2 $\text{mg}\cdot\text{g}^{-1}$ leaf mass in 2009 and 0.3 $\text{mg}\cdot\text{g}^{-1}$ leaf mass in 2010 (Figure 3.2).

Stream inputs of terrestrial invertebrates

Data from floating pan traps showed that riparian vegetation contributed terrestrial invertebrates to streams all summer long. Fifteen orders of terrestrial invertebrates were identified in pan trap samples with wasps, flies (Diptera) and spiders being the most abundant taxa by biomass (Table 3.3). Spiders, centipedes (Chilopoda), beetles (Coleoptera) and psocopterans (Psocoptera) were more abundant in the Campbell Creek, while Chester Creek pan traps collected more flies and true bugs (Table 3.3). EBC sites supported fewer moths and wasps than native sites in both streams. Sawfly larvae (Tenthredinidae) were the most abundant taxa in mixed native sites, accounting for 45% of total biomass at Campbell Creek and 35% of total biomass at Chester Creek (Table 3.3).

Biomass of terrestrial invertebrates inputs collected by pan traps did not vary significantly by stream ($F_{1,52} = 1.06$, $P = 0.309$) or by site x date interaction ($F_{6,52} = 2.09$,

$P = 0.070$), but did vary significantly by site (EBC vs. native) nested within stream ($F_{2,52} = 5.65$, $P = 0.006$) and by date ($F_{6,52} = 4.21$, $P = 0.002$). Pan traps located under riparian EBC collected significantly lower biomass of terrestrial invertebrates than pan traps placed underneath mixed native vegetation. This pattern was observed on both Campbell Creek ($P < 0.001$) and Chester Creek ($P < 0.001$) (Figure 3.3). EBC pan traps collected a mean biomass of 11.2 $mg \cdot m^{-2} \cdot day^{-1}$ in Campbell Creek and 12.0 $mg \cdot m^{-2} \cdot day^{-1}$ in Chester Creek while mixed native pan traps collected a mean biomass of 26.7 $mg \cdot m^{-2} \cdot day^{-1}$ in Campbell Creek and 35.5 $mg \cdot m^{-2} \cdot day^{-1}$ in Chester Creek (Figure 3.3).

Juvenile coho salmon ingestion of terrestrial invertebrates

Terrestrial invertebrates composed an important component of juvenile coho salmon diet. Terrestrial invertebrates accounted for 19 – 30% of overall biomass of coho diet in 2009 and 27 – 40 % of coho diet in 2010 (Figure 3.4). In 2009, coho fed primarily on adult wasps, beetles, spiders and slugs (Gastropoda) (Table 3.2). In 2010, terrestrial slugs were by far the most abundant taxa by biomass, composing 48% to 73% of the terrestrial invertebrate biomass consumed by coho salmon in these streams (Table 3.3).

No clear differences between vegetation types were detected in the amount of terrestrial invertebrate biomass ingested by juvenile coho salmon. In 2009, there were no significant effects of stream ($F_{1,224} = 4.90$, $P = 0.270$), sites nested within stream (EBC vs. native) ($F_{2,224} = 1.25$, $P = 0.289$), date ($F_{6,224} = 2.59$, $P = 0.443$), or site x date interaction ($F_{6,224} = 0.99$, $P = 0.433$). In 2009, coho in Campbell Creek consumed a higher biomass of terrestrial invertebrates in the EBC site (6.7 $mg \cdot fish^{-1}$) than in the native site (3.8 $mg \cdot fish^{-1}$) but this difference was not significant ($P = 0.101$) (Figure 3.5). In Chester Creek, coho ingested a similar biomass of terrestrial invertebrates between the EBC site (2.2 $mg \cdot fish^{-1}$) and the native site (2.5 $mg \cdot fish^{-1}$) with no significant effect of site ($P = 0.131$) (Figure 3.5). In 2010, coho consumed more terrestrial invertebrate biomass than in the previous year, but again we did not detect an effect of EBC on the biomass consumed by coho. In Campbell Creek we observed the reverse of 2009, where coho consumed a higher biomass of terrestrial invertebrates in the native site (8.0

mg·fish^{-1}) compared to the EBC site (6.4 mg·fish^{-1}) while in Chester Creek coho consumed slightly more biomass in the EBC site (8.6 mg·fish^{-1}) than the native site (5.6 mg·fish^{-1}) (Figure 3.5), although these differences were not statistically significant. Similar to 2009, in 2010 terrestrial invertebrate biomass in coho diet did not vary significantly by stream ($F_{1,175} = 0.15$, $P = 0.698$), site nested within stream ($F_{2,175} = 0.51$, $P = 0.600$), or by site x date interaction ($F_{5,175} = 0.76$, $P = 0.576$), but did vary significantly by date ($F_{5,175} = 7.74$, $P < 0.001$).

Community structure and overlap between prey availability and coho diet

The composition of terrestrial invertebrate communities varied between the 2009 and 2010 field seasons influencing their community structure and overlap. In 2009, both the cluster analysis and NMDS ordination found the terrestrial invertebrate communities present in coho diets were more similar between watersheds (Campbell vs. Chester) than vegetation type (EBC vs. native) (Figure 3.6). Communities associated with spruce branches appeared to link closely with coho diet in Campbell Creek sites, while birch and EBC branches linked more closely with coho diet in Chester Creek sites and alder appeared to be offset from the rest (Figure 3.6). In 2010, the cluster analysis and NMDS ordination plots show greater separation than in 2009. Terrestrial invertebrate communities associated with native riparian tree branches (alder, birch and spruce) were closely related to the invertebrate communities collected by pan traps in mixed native sites for both Campbell and Chester creeks (Figure 3.7). Terrestrial invertebrates associated with EBC branches were closely related to the invertebrates collected by pan traps in EBC sites for both Campbell Creek and Chester Creek. However, invertebrates consumed by juvenile coho salmon were offset from invertebrates associated with branches and pan traps of both EBC and native vegetation types (Figure 3.7). Again, invertebrates present in coho diet for both streams appeared to be more closely related by stream than by vegetation type (Figure 3.7).

Overlap of terrestrial invertebrate communities calculated by percent similarity index (PSI) values supported the patterns observed in the cluster analysis and NMDS ordination. Overall, terrestrial invertebrate communities were more similar between branches and coho diet for both EBC and native vegetation in 2009 than in 2010 (Table 3.4). In 2009, terrestrial invertebrate overlap between branches and coho diet was greater with native branches than EBC in Campbell Creek (72% mixed native vs. 50% EBC) but smaller in Chester Creek (46% mixed native vs. 57% EBC) (Table 3.4). Overlap decreased in 2010, with terrestrial invertebrates on EBC branches having greater overlap with coho diet by 37% in Campbell Creek and 32% in Chester Creek, more so than native branches and pan traps in both streams (Table 3.4).

Discussion

This study showed that terrestrial invertebrates are an important prey source for juvenile coho salmon, linking riparian forests to stream consumers. In Campbell and Chester creeks, we found riparian EBC negatively affected the abundance of terrestrial invertebrates, supporting a significantly lower biomass on the foliage of riparian tree branches compared to native deciduous trees alder and birch. All deciduous species sampled (EBC and native) supported a higher biomass than spruce. These patterns were nearly identical during the 2009 and 2010 field seasons. Our data align with previous studies finding that different plant species support varying levels of invertebrate abundance, with deciduous species generally supporting a higher biomass than conifers (Mason and MacDonald 1982; Wipfli 1997; Allan et al. 2003). In 2010, we documented that patches of riparian EBC contributed a significantly lower biomass of terrestrial invertebrate inputs to streams than patches of mixed native vegetation in both Campbell and Chester creeks. These results support our hypothesis that EBC negatively affects terrestrial invertebrate abundance and are supported by other studies finding that invasive riparian plants negatively affected terrestrial invertebrate abundance and inputs to streams (Herrera and Dudley 2003; Greenwood et al. 2004; Gerber et al. 2008).

While we documented that riparian EBC negatively affected the availability of terrestrial invertebrates, EBC did not appear to affect prey intake of terrestrial invertebrates by juvenile coho salmon. Terrestrial invertebrates composed a substantial component of juvenile coho salmon diet in our study streams, accounting for 20-30% in 2009 and 30-40% in 2010, although patterns suggest that EBC did not negatively affect the proportion of terrestrial invertebrates in coho diet. Coho also consumed a higher mean biomass of terrestrial invertebrates in 2010 than in 2009. However, no clear pattern existed between riparian vegetation type (EBC vs. native) and the biomass of terrestrial invertebrates consumed by juvenile coho salmon. The fact that patterns differed between streams and years further indicates that riparian EBC did not have a strong influence on prey intake by these stream fishes.

While these results do not support the hypothesis that riparian EBC affects prey intake by fish, but similar patterns have been documented by several other studies. In southeast Alaska, while terrestrial invertebrate abundance on branches and inputs to streams were higher on deciduous trees than conifers, there were no significant differences in terrestrial invertebrate consumption by several species of salmonids between younger alder-dominated deciduous forests and old growth conifer forests (Wipfli 1997; Allan et al. 2003). Romero et al. (2005) observed similar patterns in coastal Oregon streams where riparian vegetation types supported different abundance levels of terrestrial invertebrates, but cutthroat trout diet did not vary in streams lined by different riparian canopies. Finally, Kawaguchi and Nakano (2001) also documented that prey intake by rainbow trout did not differ between forested and grassland reaches of stream in Japan.

There may be several explanations for why we detected no effect of riparian EBC on terrestrial prey ingested by coho salmon in this study. One, coho salmon are drift-feeders and may have relied more on terrestrial invertebrates drifting downstream through our sampling sites than local inputs from the adjacent riparian vegetation (Johnson and Ringler 1980). Thus, even though coho salmon were sampled in a reach of stream lined by EBC, coho were more likely feeding on a mix of prey composed by a combination of local inputs and what drifted into a site. In addition to this mixing within the stream channel, prey mixing could have also occurred in the terrestrial environment via wind or insect dispersal further obscuring the effect of riparian EBC on terrestrial prey for fish. Allan et al. (2003) highlighted prey mixing as a potential reason why they were unable to document an effect of riparian vegetation on salmonids in southeast Alaska.

Studies by Piccolo and Wipfli (2002), Wipfli and Gregovich (2002) and Wipfli and Musslewhite (2004) found that headwater streams provide a source of invertebrates for downstream consumers. If coho were indeed relying on upstream subsidies of prey drifting downstream, it suggests that riparian vegetation further upstream could be their primary source of prey. Thus, while we sampled sites that were dominated by EBC, there still could be enough native vegetation in the upper reaches of these systems contributing a greater amount of terrestrial invertebrates and therefore not disrupting broader terrestrial prey resources for fish. Also, taking into account that EBC is currently distributed in the lower, downstream portions of each of these watersheds, it is unlikely that EBC is disrupting the upstream subsidies of terrestrial prey. However, EBC could be problematic if it continues to spread further upstream towards the headwaters of these watersheds.

Second, fish may be receiving prey from sources other than riparian trees. Our sampling methods focused exclusively on terrestrial invertebrates associated with riparian trees and did not sample invertebrates present on other vegetation types including shrubs, forbs or grasses, or the forest litter and soil. Previous studies have documented that grasses and deciduous shrubs were important sources of invertebrates to streams (Kawaguchi and Nakano 2001; Allan et al. 2003). In our study, we observed that terrestrial slugs (Gastropoda) accounted for the majority (48% to 73%) of the biomass consumed by juvenile coho salmon in 2010. However, slugs were largely absent from our branch and pan trap samples. This could be because slugs often inhabited lower habitats including lower-growing understory (Roon personal observation).

Another contributing factor could be that there were no natural barriers blocking movement of fish between EBC and native study sites in our streams. Coho could be feeding in habitats of higher resources and just happened to be present while we were sampling at a given site. Coho could also be moving between sites and although we sampled fish in the EBC site, we do not know whether the diet was truly representative of the prey available in that site.

We also conducted community analyses to see if EBC differed in community structure or overlapped less with coho diet relative to native trees. Cluster analysis and NMDS ordination techniques revealed that terrestrial invertebrate communities shifted in structure between years. In 2009, terrestrial invertebrate communities were more similar in structure between riparian vegetation and coho diet with no clear effect of EBC (Figure 3.6). However in 2010, we observed greater divergence in the structure of terrestrial invertebrate communities. Terrestrial invertebrates associated with native branches grouped more closely with pan traps in native sites, EBC branches grouped closely with pan traps in EBC sites and coho diets grouped separately (Figure 3.7). The fact that terrestrial invertebrate communities associated with EBC differed in composition from native branches in 2010 suggests that EBC may be negatively affecting terrestrial invertebrate communities, but these effects did not appear to influence terrestrial invertebrates present in coho diets.

Overlap between vegetation type and coho diet quantified by PSI values support the patterns observed in cluster analysis and NMDS ordinations. In 2009, PSI values ranged between 32 and 72% while in 2010 overlap was substantially lower ranging between 15 and 36%. Terrestrial invertebrates associated with EBC overlapped with coho diet less than native vegetation in Campbell Creek in 2009, but patterns show EBC overlapped with coho diet at similar levels or more than the native vegetation in other sites and other years. As a result, PSI values did not show any clear negative effect of EBC on coho diet relative to native vegetation in our study.

Our data showed differences in terrestrial invertebrate community structure and overlap with coho diet between years. These differences in terrestrial invertebrate community composition between years could be due to annual climatic variation that shifted a few key taxa (Schowalter et al. 1986; Danks 1992; Progar and Schowalter 2002). In 2009, the summer was warmer and drier (May – September 2009: 16.6 ºC mean air temperature, 17.2 cm of precipitation, National Weather Service, Anchorage, AK).

Aphids were abundant on all deciduous tree species (EBC and native), which in turn also increased the abundance of parasitoid wasps feeding on aphids. As a result, juvenile coho salmon fed on an increased abundance of adult wasps, overlapping more with communities on riparian branches. In 2010, the summer was cooler and wetter (May – September 2010: 15.5 ºC mean air temperature, 22.7 cm of precipitation, National Weather Service, Anchorage, AK). As a result, we observed decreases in aphid and parasitoid wasp abundance. We also observed increases in sawfly larvae abundance on native branches and pan traps and increases in terrestrial slugs in coho salmon diet. These shifts could have accounted for greater separation in community structure and decreases in overlap between invertebrates associated with riparian vegetation and coho diet.

While riparian EBC does not appear to be currently affecting terrestrial prey abundance ingested by juvenile coho salmon, there is concern that as EBC spreads throughout the drainage it could reduce the inputs of terrestrial invertebrates into streams and affect their availability as prey for fish at a much broader spatial scale. As mentioned earlier, terrestrial invertebrates accounted for a substantial portion of coho salmon diet in our study, comprising 20-30% of their diet in 2009 and 30 – 40 % of their diet in 2010. Over time, the spread of EBC could remove this component of their diet and could have a variety of ecological consequences. Research by Kawaguchi et al. (2003) indicated that experimentally reducing terrestrial inputs to streams decreased the abundance and distribution of rainbow trout. While we did not measure these population level metrics between our study sites, reducing terrestrial prey may have similar effects on coho salmon in these streams.

The reduction of terrestrial invertebrate inputs to streams could also force coho to feed more heavily on aquatic invertebrates, affecting stream invertebrate communities. It is unknown if aquatic invertebrate production in these streams is high enough to support an increase in predation by 40%. A study by Nakano et al. (1999a) found that reducing stream inputs of terrestrial invertebrates increased salmonid predation on aquatic invertebrate herbivores increasing the growth of benthic algae. A related study observed that the invasion of non-native rainbow trout in Japanese streams competed with Dolly

Varden charr for terrestrial invertebrates, forcing Dolly Varden to feed more heavily on aquatic invertebrates and decreasing the emergence of adult life stages of aquatic invertebrates (Baxter et al. 2004). This decrease in aquatic invertebrate emergence impacted riparian predators including spiders and birds (Baxter et al. 2004; Nakano and Murakami 2001). It is unknown what repercussions may occur with the future spread of EBC, but these studies suggest that it could impact both aquatic and terrestrial organisms linked through stream-riparian food webs (Baxter et al. 2005).

The further spread of EBC could impact coho salmon to a greater degree if it interacts with other ecosystem stressors inherent in these systems (Fausch et al. 2010). Other potential factors could include the simultaneous loss of native alder due to a canker and defoliation by the invasive green alder sawfly (*Monsoma pulveratum*) (Ruess et al. 2009). Not only is alder an important food source for terrestrial invertebrate prey communities as documented by this study and others (e.g. Allan et al. 2003), riparian alder is an important source of nitrogen for stream ecosystems (Helfield and Naiman 2002). This loss of riparian alder could decrease ecosystem productivity of these streams. Degradation of stream habitat through urbanization could also interact with the previously mentioned factors, accentuating the potential effects of EBC on salmonid food webs (Baxter et al. 2005; Fausch et al. 2010).

In Alaska and throughout the Pacific Ocean, Pacific salmon (*Oncorhynchus* spp.) are important cultural, economic and ecological resources. Many Pacific salmon populations are currently experiencing significant population declines, and concern has been raised that invasive species could be a contributing factor (Baxter et al. 2005, Sanderson et al. 2009). Our results suggest that riparian EBC may be disrupting ecological processes between linked stream-riparian ecosystems by reducing the abundance of terrestrial invertebrate prey resources and their inputs into streams relative to native riparian trees. While we did not detect an effect of riparian EBC on prey intake by juvenile coho salmon, lowered prey abundance as measured in this study may have long-term consequences for stream salmonids as EBC continues to spread over time.

Acknowledgements

We thank Dustin Merrigan, John Hill, Steve Ewest, Rebecca Mierzejewski, Uinniq Ahgeak and Thomas Robertson for assistance with field and laboratory work. Thanks to the members of the Wipfli aquatics lab at UAF for advice and support throughout the project. Thanks to the US Fish and Wildlife Service, USDA Forest Service, Department of Biology and Wildlife at UAF, Institute of Arctic Biology, and Alaska EPSCoR for funding this project. This work was covered under IACUC protocol 08-28.

References

Alaska Natural Heritage Program. 2006. Non-Native Species of Alaska: European Bird Cherry (*Prunus padus* L.). http://akweeds.uaa.alaska.edu.

Allan, J.D., Wipfli, M.S., Caouette, J.P., Prussian, A., and Rodgers, J. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Canadian Journal of Fisheries and Aquatic Sciences. **60**: 309-320.

Baxter, C.V., Fausch, K.D., Murakami, M., and Chapman, P.L. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology. **85**: 2656-2663.

Baxter, C.V., Fausch K.D., and Saunders, W.C. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology. **50**: 201-220.

Carlson, M.L., Lapina, I.V., Shephard, M., Conn, J.S., Densmore, R., Spencer, P., Heys, J., Riley, J., and Nielsen, J. 2008. Invasiveness ranking system for non-native plants of Alaska. USDA Forest Service, R10, R10-TP-143, p 218.

Danks, H.V. 1992. Arctic insects as indicators of environmental change. Arctic **45**: 159-166.

Dukes, J.S., and Mooney, H.A. 2004. Disruption of ecosystem processes in western North America by invasive species. Natural History Review of Chile. **77**: 411-437.

Eberle, L.C., and Stanford, J.A. 2010. Importance and seasonal availability of terrestrial invertebrates as prey for juvenile salmonids in floodplain spring brooks of the Kol River (Kamchatka, Russia Federation). River Research and Applications. **26**: 682-694.

Edwards, E., and Huryn, A. 1995. Annual contribution of terrestrial invertebrates to a New Zealand trout stream. New Zealand Journal of Marine and Freshwater Research. **29**: 467-477.

Fausch, K.D., Baxter, C.V., and Murakami, M. 2010. Multiple stressors in north temperate streams: lessons from linked forest-stream ecosystems in northern Japan. Freshwater Biology. **55**: 120-134.

Flagstad, L.A., Cortés-Burns, H., and Roberts, T.L. 2010. Invasive plant inventory and bird cherry control trials phase II: bird cherry distribution, demography, and reproduction biology along Chester and Campbell Creek trails, Anchorage, Alaska. Alaska Natural Heritage Program, p. 61.

Friedman, J.M., Auble, G.T., Shafroth, P.B., Scott, M.L., Merigliano, M.F., Freehling, M.D., and Griffin, E.R. 2005. Dominance of non-native riparian trees in western USA. Biological Invasions. **7**: 747–751.

Gerber, E., Krebs, C., Murrell, C., Moretti, M., Rocklin, R., and Schaffner, U. 2008. Exotic invasive knotweeds (*Fallopia* spp.) negatively affect native plant and invertebrate assemblages in European riparian habitats. Biological Conservation. **141**: 646-654.

Glova, G., and Sagar, P. 1994. Comparison of fish and macroinvertebrate standing stocks in relation to riparian willows (*Salix* spp.) in three New Zealand streams. New Zealand Journal of Marine and Freshwater Research. **28**: 255-266.

Greenwood, H., O'Dowd D.J., and Lake, P.S. 2004. Willow (*Salix rubens*) invasion of the riparian zone in south-eastern Australia: reduced abundance and altered composition of terrestrial arthropods. Diversity and Distributions. **10**: 485-492.

Gregory, S.V., Swanson, F.J., McKee W.A., and Cummins, K.W. 1991. An ecosystem perspective of riparian zones. BioScience. **41**: 540-551.

Helfield, J.M, and Naiman, R.J. 2002. Salmon and alder as nitrogen sources to riparian forests in a boreal Alaskan watershed. Oecologia. **133**: 573-582.

Herrera, A.M., and Dudley T.L. 2003. Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (*Arundo donax*) invasion. Biological Invasions. **5**: 167-177.

Hierro, J.L., and Callaway, R.M. 2003. Allelopathy and exotic plant invasion: from molecules and genes to species interactions. Plant and Soil. **256**: 29-39.

Hood, W.G., and Naiman, R.J. 2000. Vulnerability of riparian zones to invasion by exotic vascular plants. Plant Ecology. **148**: 105-114.

Hurlbert, S.H. 1978. The measurement of niche overlap and some relatives. Ecology. **9**: 67-77.

Johnson, J.H., and Ringler, N.H. 1980. Diets of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*) relative to prey availability. Canadian Journal of Zoology. **58**: 553-558.

Kawaguchi, Y., and Nakano, S. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. Freshwater Biology. **46**: 303-316.

Kawaguchi, Y., Taniguchi, H., and Nakano, S. 2003. Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. Ecology. **84**: 701-708.

Kennedy, T.A., Finlay, J.C., and Hobbie, S.E. 2005. Eradication of invasive *Tamarix ramosissima* along a desert stream increases native fish density. Ecological Applications. **15**: 2072-2083.

Leather, S.R., 1996. *Prunus padus* L. Journal of Ecology. **84**: 125-132.

Mason, C.F., and MacDonald, S.M. 1982. The input of terrestrial invertebrates from tree canopies. Freshwater Biology. **12**: 305-311.

Milner, A.M., and Oswood, M.W. 2000. Urbanization gradients in streams of Anchorage, Alaska: a comparison of multivariate and multimetric approaches to classification. Hydrobiologia. **422**: 209-223.

Nakano, S., Miyasaka, H., and Kuhara, N. 1999a. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology. **80**: 2435-2441

Nakano, S., Kawaguchi, Y., Taniguchi, Y., Miyasaka, H., Shibata, Y., Urabe, H., and Kuhara, N. 1999b. Selective foraging on terrestrial invertebrates by rainbow trout in a forested headwater stream in northern Japan. Ecological Research. **14**: 351-360.

Nakano, S., and Murakami, M. 2001. Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences. **98**: 166-170.

Ober, H.K., and Hayes, J.P. 2008. Influence of forest riparian vegetation on abundance and biomass of nocturnal flying insects. Forest Ecology and Management. **256**: 1124-1132.

Ourso, R.T., and Frenzel, S.A. 2003. Identification of linear and threshold responses in streams along a gradient of urbanization in Anchorage, Alaska. Hydrobiologia. **501**: 117-131.

Piccolo, J.J., and Wipfli, M.S. 2002. Does red alder (*Alnus rubra*) in upland riparian forests elevate macroinvertebrate and detritus export from headwater streams to downstream habitats in southeastern Alaska? Canadian Journal of Fisheries and Aquatic Sciences. **59**: 503-513.

Planty-Tabacchi, A.M., Tabacchi, E., Naiman, R.J., Deferrari, C., and Décamps, H. 1996. Invasibility of species-rich communities in riparian zones. Conservation Biology. **10**: 598–607.

Progar, R.A., and Schowalter, T.D. 2002. Canopy arthropod assemblages along a precipitation and latitudinal gradient among Douglas-fir *Pseudotsuga menziesii* forests in the Pacific Northwest of the United States. Ecography **25**: 129 -138.

Ringold, P.L., Magee, T.K., and Peck, D.V. 2008. Twelve invasive plant taxa in US western riparian ecosystems. Journal of North American Benthological Society. **27**: 949-966.

Romero, N., Gresswell, R.E., and Li, J.L. 2005. Changing patterns in coastal cutthroat trout (*Oncorhynchus clarki clarki*) diet and prey in a gradient of deciduous canopies. Canadian Journal of Fisheries and Aquatic Sciences. **62**: 1797-1807.

Ruess, R.W., McFarland, J.M., Trummer, L.M., and Rohrs-Richey, J.K. 2009. Disease-mediated declines in N-fixation inputs by *Alnus tenuifolia* to early-successional floodplains in interior and south-central Alaska. Ecosystems. **12**: 489-502.

Sabo, J.L., Bastow, J.L., and Power, M.E. 2002. Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. Journal of the North American Benthological Society. **21**: 336-343.

Sample, B.E., Cooper, R.J., Greer, R.D., and Whitmore, R.C. 1993. Estimation of insect biomass by length and width. American Midland Naturalist. **129**: 234-240.

Sanderson, B.L., Barnas, K.A., and Rub, A.W. 2009. Nonindigenous species of the Pacific Northwest: an overlooked risk to endangered salmon? BioScience. **59**: 245-256.

Schowalter, T.D., Hargrove, W.W., Crossley Jr., D.A., 1986. Herbivory in forested ecosystems. Annual Review of Entomology. **31**: 177–196.

Sher, A.A., Marshall, D.L., and Taylor, J.P. 2002. Establishment patterns of native *Populus* and *Salix* in the presence of invasive nonnative *Tamarix*. Ecological Applications. **12**: 760–772.

Wiesenborn, W.D. 2005. Biomass of arthropod trophic levels on *Tamarix ramosissima* (Tamaricaceae) branches. Environmental Entomology. **34**: 656-663.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., and Losos, E. 1998. Quantifying threats to imperiled species in the United States. BioScience. **48**: 607-615.

Wipfli, M.S., 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences. **54**: 1259-1269.

Wipfli, M.S., and Gregovich, D.P. 2002. Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. Freshwater Biology. **47**: 957-969.

Wipfli, M.S., and Musslewhite, J. 2004. Density of red alder (*Alnus rubra*) in headwaters influences invertebrate and detritus subsidies to downstream fish habitats in Alaska. Hydrobiologia. **520**: 153-163.

Table 3.1. Characteristics of EBC and native vegetation study sites in Campbell and Chester creeks.

	Campbell Creek		**Chester Creek**	
Parameter	**EBC Site**	**Native Site**	**EBC Site**	**Native Site**
Elevation (m)	27	29	35	36
Reach Length (m)	139	143	166	162
Stream Width (m)	9.6	9.6	4.7	3.8
Discharge ($m^3 \cdot s^{-1}$)	2.7	2.5	0.6	0.5
Stream Temperature (˚C)	9.3	9.4	11.6	11.9
pH	7.9	8.0	7.7	7.6
Conductivity ($\mu S \cdot cm^{-1}$)	118	122	256	258
Dissolved Oxygen ($mg \cdot L^{-1}$)	10.4	10.6	11.4	11.4
Canopy Cover (%)	30.7	21.4	53.9	26.5
EBC Cover (%)	77.6	9.2	88.1	5.8
Canopy Composition*	E>S>A>B	S>A>B>E	E>S>B>A	S>B>A>E
Fish fork length (mm)	81.5	79.8	83.3	88.3
Fish mass (g)	6.2	6.6	7.3	8.4

* Canopy composition abbreviations include: Alder (A), Birch (B), European bird cherry (E), and Spruce (S).

Table 3.2. Terrestrial invertebrate community composition in 2009. The percent composition by biomass (mg) of terrestrial invertebrate communities that were associated with the foliage of riparian tree branches and consumed by juvenile coho salmon in Campbell and Chester creeks.

	Branch				**Fish Diet**			
					Campbell		**Chester**	
Taxon	**Alder**	**Birch**	**EBC**	**Spruce**	**EBC**	**Native**	**EBC**	**Native**
Acari	0.1	0.3	0.2	0.8	0.1	0.2	0.9	0.6
Arachnida	2.3	7.4	10.6	39.5	16.5	14.8	8.2	3.1
Coleoptera	6.1	0.8	3.7	6.8	7.6	9.5	25.4	22.3
Collembola	0.1	0.1	0.5	1.8	0.4	0.6	2.3	1.2
Diptera	0.5	0.2	0.7	0.6	8.1	3.1	7.3	6.0
Gastropoda	0	0	0	0	21.0	14.0	0	6.9
Hemiptera	1.9	1.9	0	5.1	0.4	0	1.1	0
Homoptera	19.6	18.0	19.1	6.3	3.7	4.0	10.9	14.3
Hymenoptera	65.3	66.8	45.2	34.6	34.5	48.5	36.7	42.3
Lepidoptera	3.3	2.8	14.2	1.4	6.5	0.7	1.1	1.9
Neuroptera	0	1.0	0.6	0	0	0	0	0
Oligochaeta	0	0	0	0	0	0	0	0
Psocoptera	0.5	0.3	3.3	3.0	1.2	4.5	5.7	1.4
Thysanoptera	0.3	0.4	1.9	0.1	0	0.1	0.4	0

Table 3.3. Terrestrial invertebrate community composition in 2010. The percent composition by biomass (mg) of terrestrial invertebrate communities that were associated with the foliage of riparian tree branches, stream inputs collected by floating pan traps and consumed by juvenile coho salmon in Campbell and Chester creeks.

	Branch				**Pan Trap**				**Fish Diet**			
					Campbell		**Chester**		**Campbell**		**Chester**	
Taxon	**Alder**	**Birch**	**EBC**	**Spruce**	**EBC**	**Native**	**EBC**	**Native**	**EBC**	**Native**	**EBC**	**Native**
Acari	0.1	0.1	0.2	0.1	0.1	0.1	0.6	0	0.1	0.1	0.3	0.4
Arachnida	8.4	7.5	32.8	30.4	27.6	10.8	5.1	0.3	6.1	7.1	3.0	5.0
Archaeognatha	0	0	0	0	0	0	0.8	0	0	0	0	0
Chilopoda	0	0	0	0	16.8	0	0	0	2.1	0	0	0
Coleoptera	0.7	0.3	0.2	0.3	16.1	9.8	0	0	12.9	4.4	1.0	0.5
Collembola	0.3	0.3	2.4	1.8	1.1	0.3	1.6	0.5	0.1	0.4	1.1	0.3
Diptera	2.1	0.9	13.3	3.1	6.0	2.3	13.4	28.1	13.2	4.1	8.0	13.3
Gastropoda	0	0.5	10.8	0	0	0	0	0	48.4	56.3	72.6	66.7
Hemiptera	0.5	0.5	1.6	2.0	0.5	1.0	4.4	13.2	0	0	0.1	0.7
Homoptera	15.1	13.4	13.3	2.2	5.9	7.1	11.6	10.8	4.0	10.4	6.5	6.3
Hymenoptera	63.7	66.6	13.1	48.4	17.7	44.9	54.4	34.7	11.6	12.4	5.1	1.9
Lepidoptera	7.4	8.3	7.7	1.0	1.1	11.8	3.3	11.1	1.0	4.1	1.0	2.0
Neuroptera	0.2	0.1	0.9	1.0	1.1	1.8	0	0	0	0	0.8	0.4
Oligochaeta	0	0	0	0	0	0	0.6	0	0	0	0	0
Psocoptera	1.4	1.4	2.4	9.5	5.5	10.0	2.9	1.1	0.4	0.6	0.3	1.4
Thysanoptera	0.1	0.1	1.3	0.2	0.5	0.1	1.3	0.2	0.1	0.1	0.4	1.1

Table 3.4. Overlap of terrestrial invertebrate communities. The percent similarity index (% PSI) values of terrestrial invertebrates quantified between riparian vegetation type and coho diet in Campbell and Chester creeks in 2009 and 2010.

Year	**Stream**	**Comparison**	**% PSI**
2009	Campbell	EBC Branches vs. EBC Fish Diet	49.8
		Native Branches vs. Native Fish Diet	72.3
	Chester	EBC Branches vs. EBC Fish Diet	56.7
		Native Branches vs. Native Fish Diet	45.6
2010	Campbell	EBC Branches vs. EBC Fish Diet	36.6
		Native Branches vs. Native Fish Diet	23.2
	Chester	EBC Branches vs. EBC Fish Diet	32.2
		Native Branches vs. Native Fish Diet	19.5
	Campbell	EBC Pan Traps vs. EBC Fish Diet	32.3
		Native Pan Traps vs. Native Fish Diet	17.7
	Chester	EBC Pan Traps vs. EBC Fish Diets	19.0
		Native Pan Traps vs. Native Fish Diet	20.2

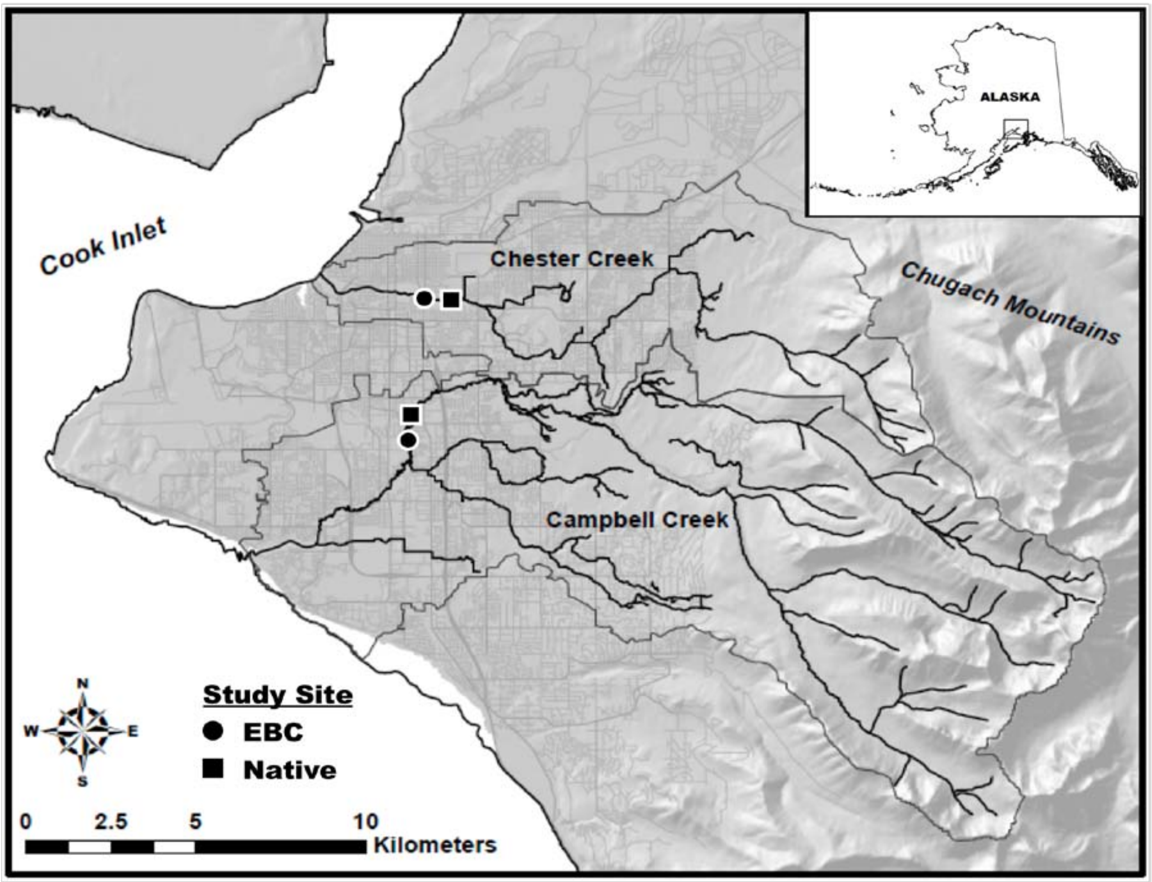

Figure 3.1. Map of EBC and native vegetation study sites in Campbell and Chester creeks.

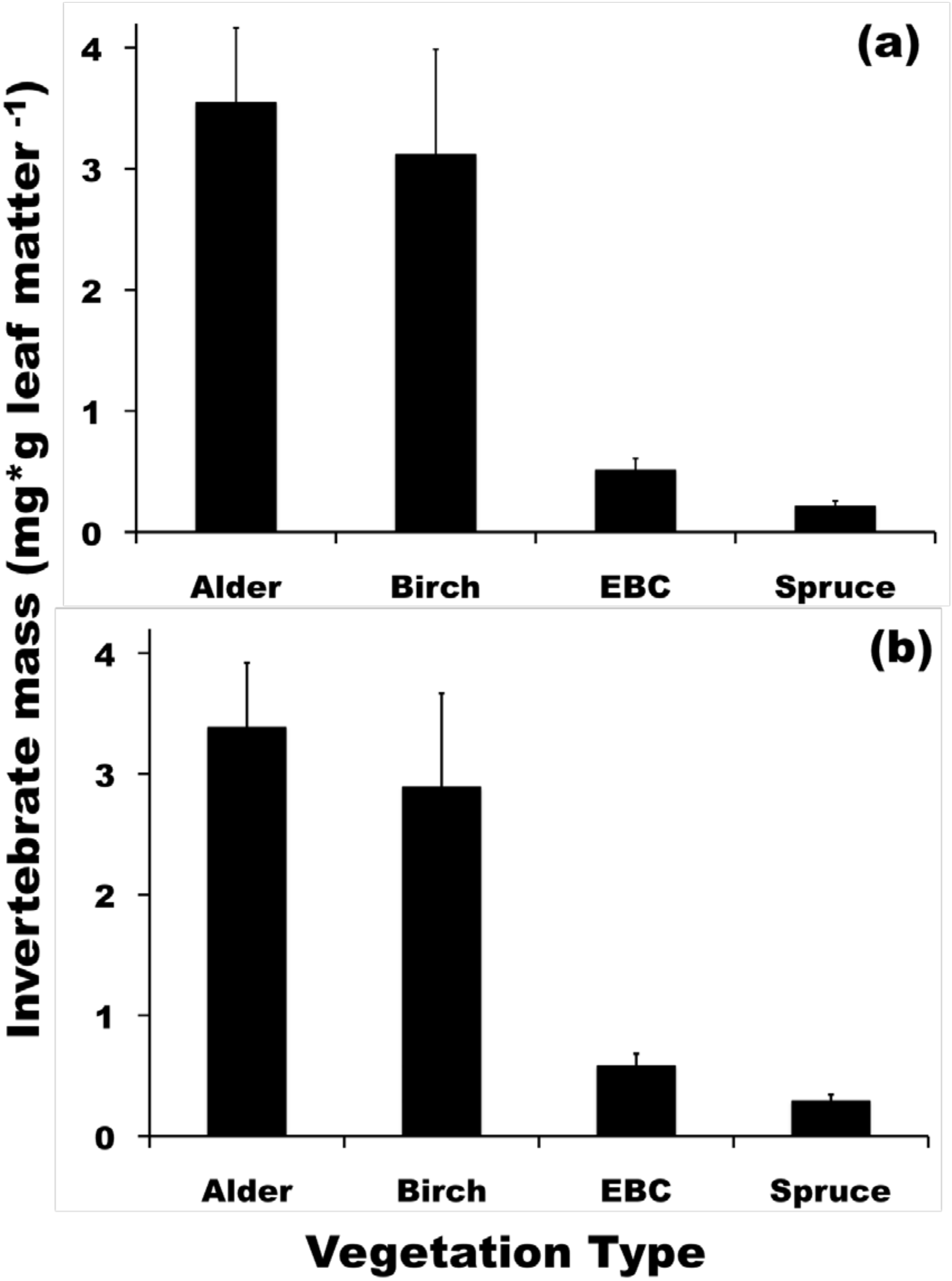

Figure 3.2. Terrestrial invertebrate biomass associated with foliage of riparian tree branches. Mean terrestrial invertebrate mass per gram of leaf matter that was associated with two native deciduous tree species (alder and birch), deciduous EBC and native conifer (spruce) in a) 2009 and b) 2010. Error bars represent standard errors.

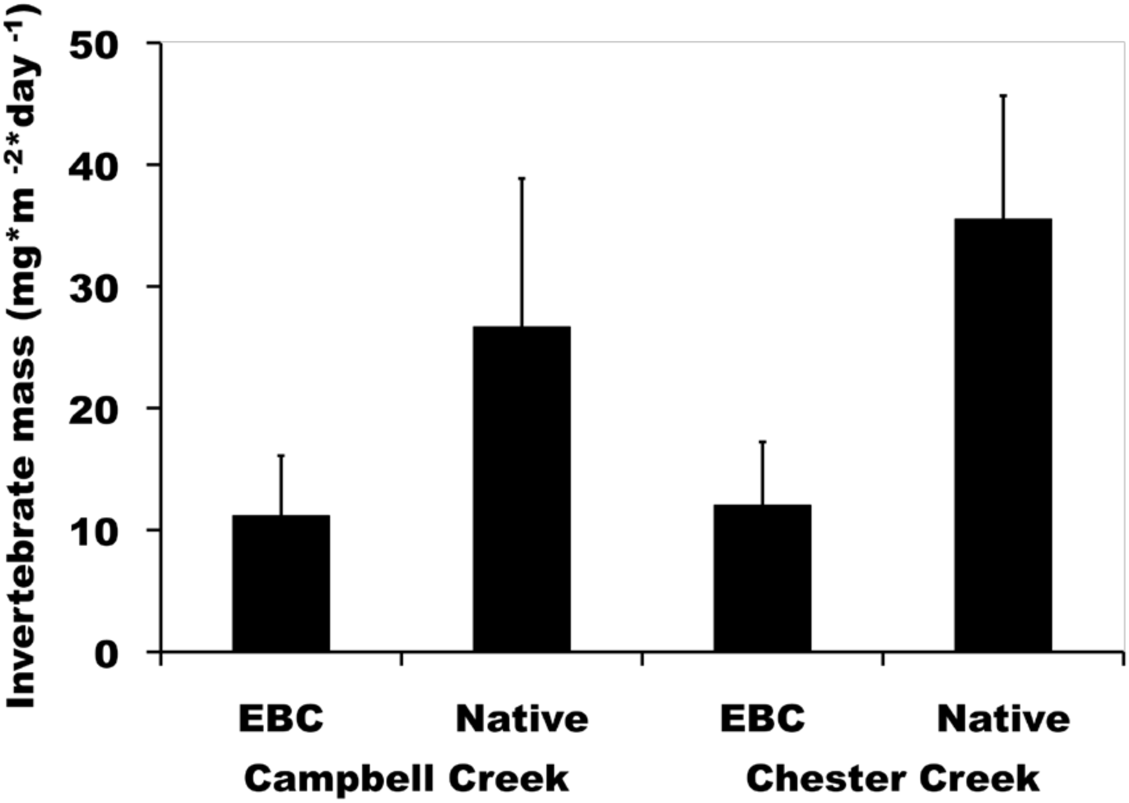

Figure 3.3. Stream inputs of terrestrial invertebrate biomass. Mean stream inputs of terrestrial invertebrate biomass that were captured in floating pan traps underneath EBC and mixed native vegetation in Campbell and Chester creeks in 2010. Error bars represent standard errors.

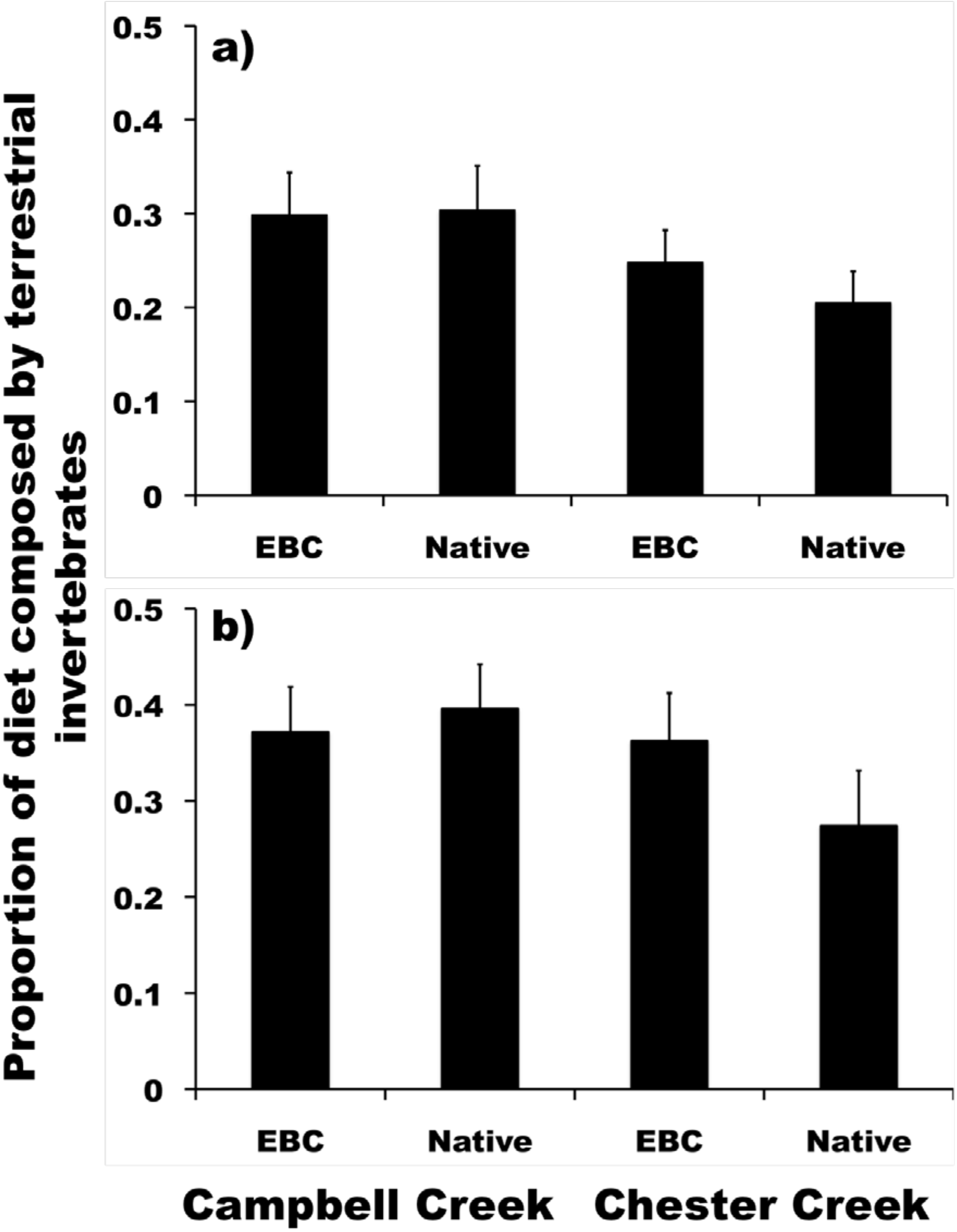

Figure 3.4. Proportion of coho diet comprised by terrestrial invertebrates. The mean proportion of coho diet comprised by terrestrial invertebrates by biomass in Campbell and Chester creeks in a) 2009 and b) 2010. Error bars represent standard errors.

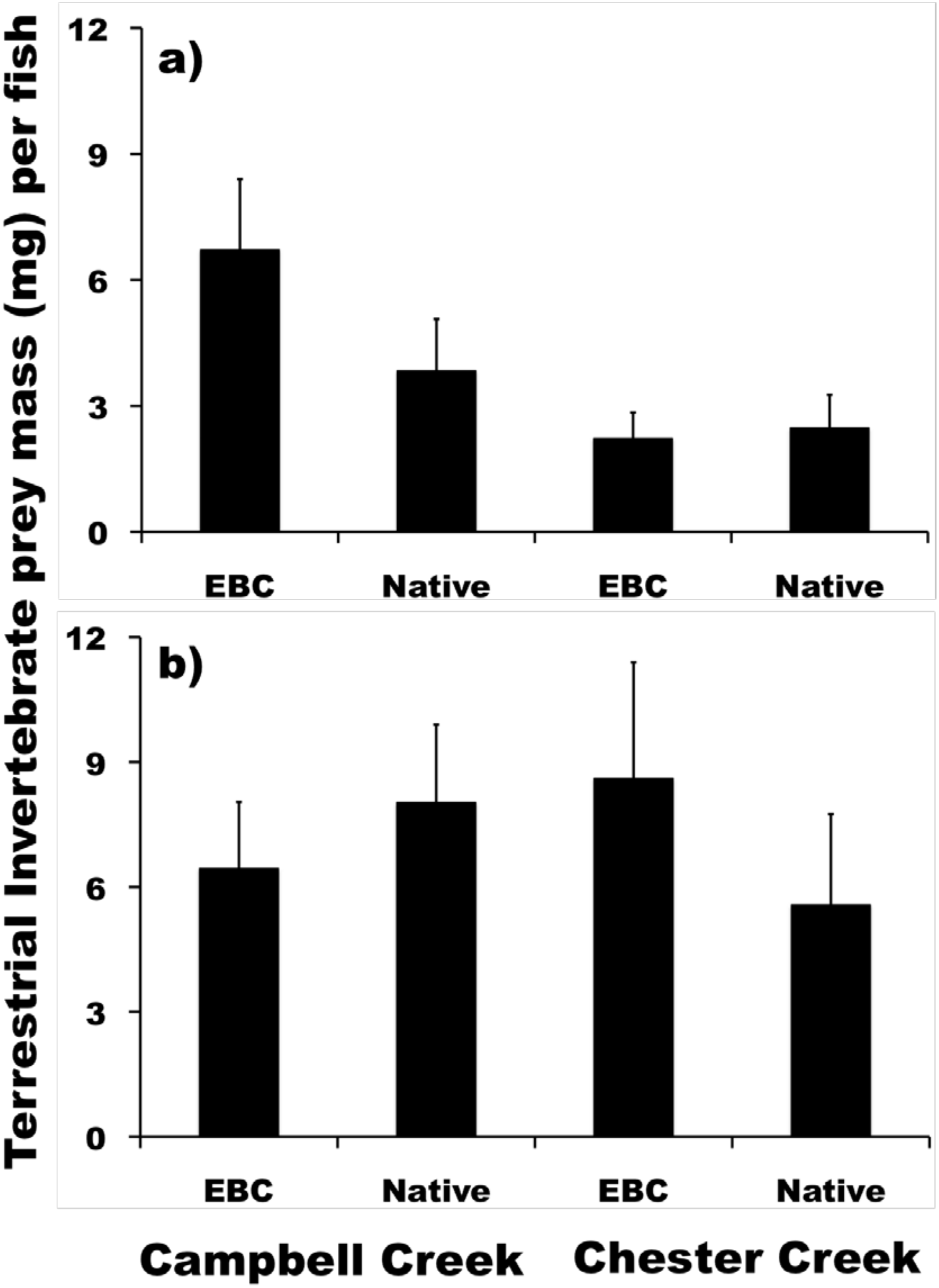

Figure 3.5. Terrestrial invertebrate biomass ingested by juvenile coho salmon. The mean biomass of invertebrates that were consumed in sites lined by EBC and native vegetation in Campbell and Chester creeks in a) 2009 and b) 2010. Error bars represent standard errors.

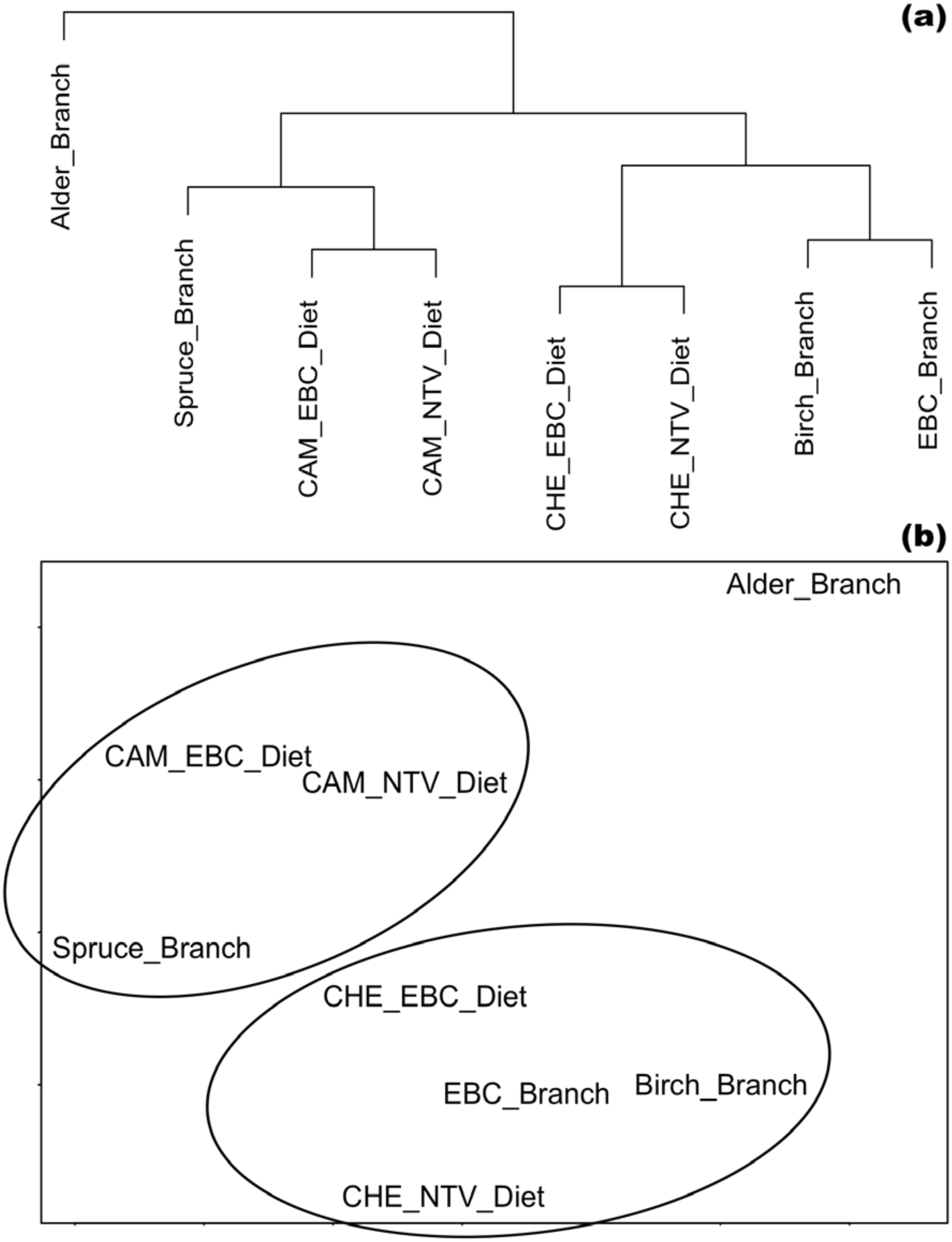

Figure 3.6. Community structure of terrestrial invertebrates in 2009. Communities that were associated with riparian tree branches and fish diet. (a) cluster analysis and (b) NMDS ordination. Abbreviation codes: CAM = Campbell Creek, CHE = Chester Creek, EBC = EBC Site, NTV = Native Site.

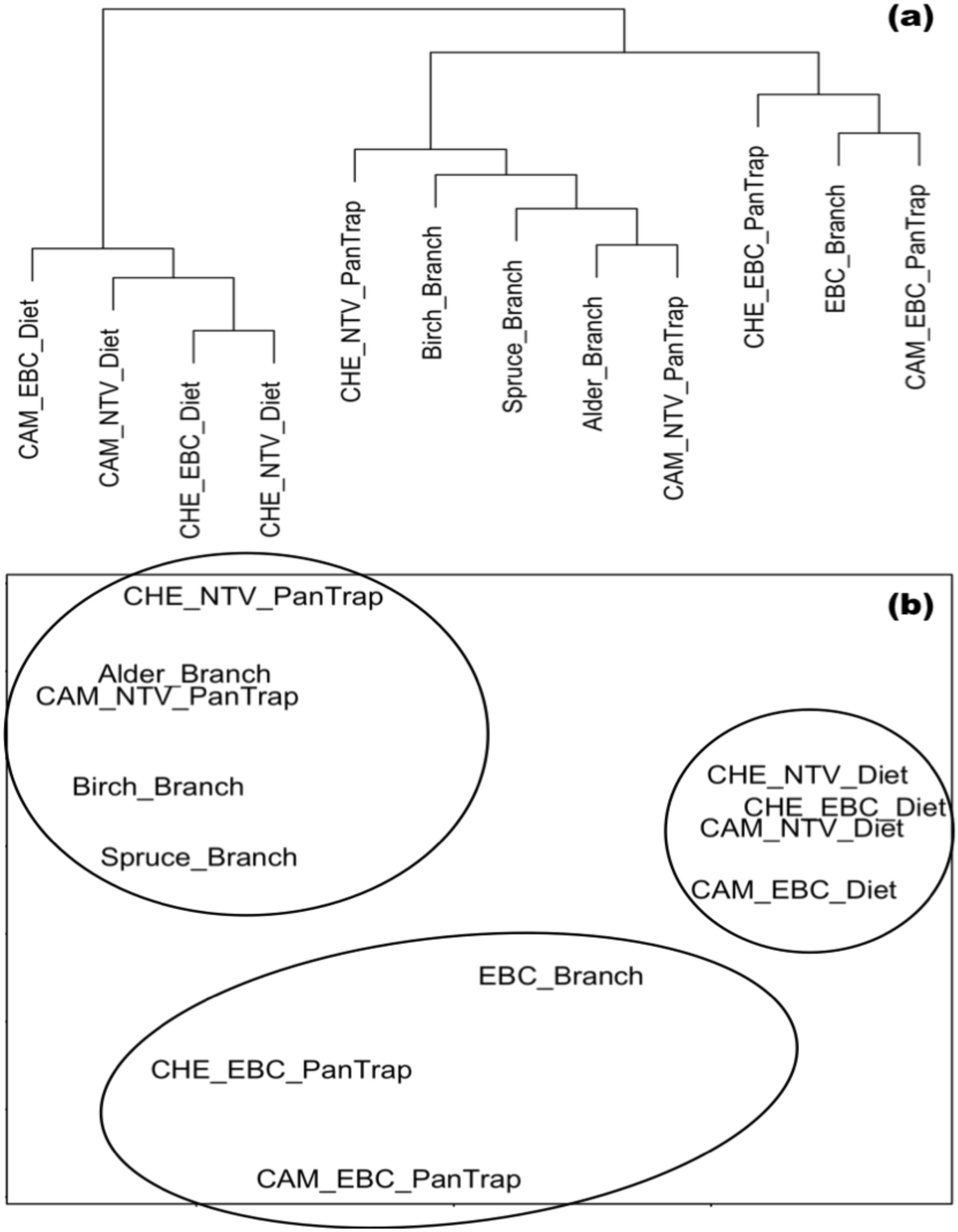

Figure 3.7. Community structure of terrestrial invertebrates in 2010. Communities that were associated with riparian tree branches, pan traps and fish diet. (a) cluster analysis and (b) NMDS ordination. Abbreviation codes: CAM = Campbell Creek, CHE = Chester Creek, EBC = EBC Site, NTV = Native Site.

Conclusion

Our studies contributed substantial new information concerning the ecological effects associated with the spread of European bird cherry in riparian forests along streams in Anchorage, Alaska.

In Chapter 1 we documented the distribution, local abundance and maturity of wild *Prunus* populations along Campbell and Chester creeks. Our surveys along these streams revealed that like Carlson and Shephard (2007) observed, the current populations of both *Prunus padus* and *Prunus virginiana* were distributed primarily within the urban extents of these watersheds. However, our results indicate that invasive *Prunus* can spread into natural habitats and locally displace native species. Combined with the high density of seedlings and its ability to access new habitats through dispersal by birds, our data suggest that *Prunus* could transform riparian forests and potentially reduce the biodiversity of these communities. Our distribution maps will provide essential baseline data for land managers as *Prunus* species continue to spread over time.

Data from our vegetation surveys suggest a few patterns that could help predict other watersheds susceptible to the spread of EBC. As mentioned before, while the current distribution of EBC appears to be largely limited to the urban extent of Campbell and Chester creeks, we also found it growing in adjacent natural habitats indicating that it is not dependent on disturbed habitats. This implies that not only could EBC continue to spread into the natural habitats of these watersheds, it could also spread into adjacent watersheds. The fact that EBC can locally displace native vegetation suggests that if left alone EBC could transform riparian forests in the wild areas of Alaska. Once it establishes itself in an adjacent watershed, mature trees could act as stepping-stones further expanding its distribution. How far EBC is able to spread will ultimately depend on how far birds are able to carry the seeds. Future research should address the species composition and behavior of birds feeding on and responsible for spreading EBC. This will be an important piece of the puzzle to better understand the future spread of EBC in Alaska.

Our next two studies examined whether riparian EBC is disrupting ecological processes linked to salmonid food webs. In Chapter 2 we conducted leaf pack experiments comparing EBC to native species in leaf litter processing by aquatic invertebrate shredders. In both experiments we observed that EBC broke down faster or at a similar rate to native alder, birch and cottonwood leaf litter. We also documented EBC leaf litter supported similar shredder communities, not differing significantly in abundance, biomass, community structure or growth. Our results suggest that EBC is functionally similar to native species of leaf litter and does not appear to be disrupting leaf litter processing by shredders in these streams. These results align with other studies looking at the effects of invasive leaf litter inputs in streams, finding that while an invasive riparian plant may change the composition of leaf litter inputs to streams, native shredders were able to utilize those resources (Lacan et al. 2010).

In Chapter 3 we evaluated if EBC affected terrestrial invertebrate prey resources for juvenile coho salmon. EBC foliage supported a significantly lower biomass of terrestrial invertebrates on riparian tree branches compared to native deciduous trees, alder and birch. EBC also contributed a significantly lower biomass of terrestrial invertebrates to streams compared to mixed native vegetation. However, while we documented that EBC disrupted the availability of terrestrial prey, we were unable to document an effect of riparian EBC on the amount of terrestrial invertebrate prey consumed by juvenile coho salmon. Community analyses did not show any clear negative effect of EBC on prey resources for fish, not differing in community structure or overlapping less with coho diet than native vegetation. While we were unable to document any effect on terrestrial prey consumed by juvenile coho, lower prey abundance measured by this study could affect fish as EBC spreads through these watersheds.

From the results of these two studies, the ecological effects associated with EBC in these watersheds appear to be mixed; they do not appear to be drastically disrupting salmonid food webs. The fact that EBC supported similar shredder communities to native species suggests that EBC is not disrupting leaf litter processing in streams and is not negatively affecting food supplies for other functional feeding groups of aquatic invertebrates. We observed that EBC disrupted the abundance and stream subsidies of terrestrial invertebrate prey, but were unable to detect an effect on coho salmon in these streams. If EBC continues to spread and further disrupts terrestrial invertebrate subsidies for stream fishes, it could cause coho to feed more heavily on aquatic taxa. It is unknown if aquatic invertebrate production is high enough in these systems to support this increased predation. Other studies investigating the effects of reductions in terrestrial invertebrate prey resources have documented consequences on both terrestrial and aquatic organisms linked through stream-riparian food webs including, decreases in emerging adult aquatic invertebrates, riparian spiders and riparian birds (Nakano et al. 1999, Kawaguchi et al. 2003, Baxter et al. 2004). The future spread of EBC could have similar effects on stream-riparian linkages connected to salmonid food webs.

The limited impacts associated with EBC could be a function of the current distribution of EBC in these watersheds. EBC is largely distributed in the downstream portions of these watersheds, while the upstream portions remain largely dominated by native vegetation. If the headwaters act as sources of invertebrate prey for salmonids further downstream (Piccolo and Wipfli 2002) it might explain why we did not observe an effect of EBC on these stream fishes. If EBC continues to spread into the headwaters of these watersheds and displaces the native vegetation, it could disrupt terrestrial invertebrate prey resources to a greater degree, negatively affecting salmonid production in these streams.

While we did not observe strong negative effects there could be other ecological consequences associated with EBC that we did not study. The simultaneous dieback of native thin-leaf alder (*Alnus tenuifolia*), could accentuate the possible impacts associated with EBC highlighted in this thesis. Riparian alder is important for stream and riparian ecosystems as a source of nitrogen (Helfield and Naiman 2002) and as a preferred food source for both aquatic and terrestrial invertebrates (Irons et al. 1988, Allan et al. 2003), supporting salmonids further downstream (Piccolo and Wipfli 2002). In this case, the loss of native alder could be more detrimental to salmonid food webs than the spread of EBC

(Lecerf et al. 2005). Future research should investigate the effects associated with the loss of riparian alder on stream food webs and watershed productivity.

Invasive species are a concern worldwide because they can displace native species, reduce biodiversity and disrupt ecological processes. In Alaska and around the Pacific Ocean, Pacific salmon are important cultural, economic, and ecological resources. Concern has been raised that invasive species could be a factor responsible for their decline (Baxter et al. 2005, Sanderson et al. 2009). In spite of this concern, few studies have attempted to relate the effects of invasive riparian plants on stream salmonids. Our data provide clues about the extent to which invasive riparian plants can affect native species and ecological processes in stream ecosystems and salmonid food webs in Alaska. These findings will also help guide the management of EBC by municipal, state and federal land management agencies involved in managing urban watersheds, fisheries and controlling invasive species. While the patterns documented in this thesis are mixed and do not show EBC to be dramatically disrupting salmonid food webs, our results suggest that EBC has the potential to do so if it continues to spread over time.

References

Allan, J.D., M.S. Wipfli, J.P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Canadian Journal of Fisheries and Aquatic Sciences 60: 309–320.

Baxter, C.V., K.D. Fausch, M. Murakami, and P.L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology 85: 2656-2663.

Baxter, C.V., K.D. Fausch, and W.C. Saunders. 2005. Tangled webs: Reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50: 201–220.

Carlson, M.L., and M. Shephard. 2007. The spread of invasive exotic plants in Alaska: is establishment of exotics accelerating? In: Harrington TB, Reichard SH (eds) Meeting the challenge: invasive plants in pacific northwestern ecosystems. USDA Forest Service PNW Research Station, Portland, pp 111–127.

Helfield, J.M, and R.J. Naiman. 2002. Salmon and alder as nitrogen sources to riparian forests in a boreal Alaskan watershed. Oecologia 133: 573-582.

Irons, J.G., M.W. Oswood and J.P Bryant. 1988. Consumption of leaf detritus by a stream shredder – influence of tree species and nutrient status. Hydrobiologia 160: 53-61.

Kawaguchi, Y., Y. Taniguchi, and S. Nakano. 2003. Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. Ecology 84: 701-708.

Lacan, I., V.H. Resh, and J.R. McBride. 2010. Similar breakdown rates and benthic macroinvertebrate assemblages on native and *Eucalyptus globulus* leaf litter in Californian streams. Freshwater Biology 55: 739-752.

Lecerf, A., M. Dobson, C.K. Dang and E. Chauvet. 2005. Riparian plant species loss alters trophic dynamics in detritus-based stream ecosystems. Oecologia 146: 432-442.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80: 2435-2441.

Piccolo, J.J. and M.S. Wipfli. 2002. Does red alder (*Alnus rubra*) in upland riparian forests elevate macroinvertebrate and detritus export to downstream habitats in southeastern Alaska? Canadian Journal of Fisheries and Aquatic Sciences 59: 503-513.

Sanderson, B.L., K.A. Barnas and A.M. Rub. 2009. Nonindigenous species of the Pacific Northwest: An overlooked risk for endangered salmon? BioScience 59: 245 -256.